

Influence of coastal upwelling–downwelling variability on tropical euphausiid abundance and community structure in the inshore Mexican central Pacific

Israel Ambriz-Arreola^{1,*}, Jaime Gómez-Gutiérrez²,
María del Carmen Franco-Gordo¹, Bertha E. Lavaniegos³, Enrique Godínez-Domínguez¹

¹Centro de Ecología Costera, Universidad de Guadalajara, Gómez Farias 82, San Patricio Melaque, Jalisco 48980, Mexico

²Centro Interdisciplinario de Ciencias Marinas, Departamento de Plancton y Ecología Marina, Ave. IPN s/n, Col. Playa Palo de Santa Rita, Apdo. Postal 592 La Paz, Baja California Sur, CP 23096, Mexico

³Departamento de Oceanografía Biológica, Centro de Investigación Científica y de Educación Superior de Ensenada, Km 107 Carretera Tijuana-Ensenada, Apdo. Postal 360, CP 22860, Ensenada, Baja California, Mexico

ABSTRACT: The effect of wind-induced coastal upwellings on tropical euphausiid abundance and community structure was investigated in the Mexican central Pacific (19° N, 105° W) during a monthly time series (1996–1998). Eight species were identified, of which *Euphausia distinguenda* contributed between 88 and 90% of the total euphausiid abundance, and *E. lamelligera* contributed ~7%. The hydrographic structure (<200 m depth) and euphausiid species composition had strong seasonality patterns associated with the upwelling (February to May) and downwelling (July to November) periods. Redundancy analysis of euphausiid abundance and community structure as a function of the environmental variables revealed that coastal upwelling index, salinity at 10 m depth, and temperature explained most of the euphausiid abundance variability. Stations sampled during intense upwelling periods had the highest abundance of *E. distinguenda* and *E. lamelligera* juveniles and adults. Their abundance was strongly and positively correlated with salinity and abundance of nano- and microphytoplankton, but was negatively correlated with surface temperature. Larvae of *E. distinguenda* and the oceanic species *Nematoscelis gracilis* (downwelling ensemble) were strongly associated with warm waters of low phytoplankton abundance. The hepato-somatic index (ratio of hepatopancreas length to carapace length) of *E. distinguenda* and *E. lamelligera* adults was significantly larger during mixed and semi-mixed than during stratified periods, providing a useful proxy for euphausiid health and trophic condition. Wind-induced upwelling–downwelling are significant coastal processes that influenced seasonal euphausiid abundance and species composition in this tropical ecosystem, while the strong and brief El Niño event of 1997–98 had only a relatively moderate effect in comparison with that observed on euphausiids from transitional (northwest of Mexico) and temperate (Pacific USA) ecosystems.

KEY WORDS: Tropical euphausiids · *Euphausia distinguenda* · *Euphausia lamelligera* · Upwelling · Downwelling · El Niño · Mexican central Pacific

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INTRODUCTION

The interaction of northwestern winds, coastline orientation, bottom topography, and regional current system induce coastal upwelling–downwelling events

along the central Pacific coast of Mexico, commonly known as the Cabo Corrientes region (Roden 1964, Torres-Orozco et al. 2005, López Sandoval et al. 2009a,b). In this tropical region, upwelling events typically occur from December to May, and are the

*Email: iambriz@costera.melaque.udg.mx

main oceanographic processes producing seasonal variability in phytoplankton photosynthetic pigments (Álvarez-Borrego 1983). Satellite ocean surface chlorophyll *a* (chl *a*) images and *in situ* chl *a* concentration measurements show that the coastal region off Cabo Corrientes exhibits strong seasonal variability (López Sandoval et al. 2009a,b). Satellite images of sea-surface temperature in the region show that the influence of upwelling events can extend about 46 km along the coast, covering an area of approximately 2586 km² (Torres-Orozco et al. 2005). The effects of these meso-scale coastal features in Cabo Corrientes on zooplankton have been studied for tropical copepods (Suárez-Morales et al. 2000), ichthyoplankton (Franco-Gordo et al. 2002, 2004, León-Chávez et al. 2010), and euphausiids (krill; Sánchez-Osuna & Hendrickx 1983, Färber-Lorda et al. 2010).

The dominant ocean circulation pattern in the Mexican central Pacific is highly variable and complex, due to the influence of the California Current, Mexican Coastal Current, and currents not easily delimited in the mouth of the Gulf of California (Wyrski 1967, Baumgartner & Christensen 1985, Kessler 2006). The Eastern Tropical Pacific (ETP) off Mexico (23 to 17° N) has a dynamic circulation characterized by substantial variability forced by atmosphere–ocean interactions at 3 main time–space scales: (1) a poleward coastal current developing during late spring and summer, while an equatorward current is observed during the rest of the year, causing significant seasonal variability in oceanographic conditions; (2) eddies, filaments, and upwelling events that cause intense mesoscale oceanographic activity over days, weeks, or even a few months; (3) the El Niño Southern Oscillation (ENSO) cycle that causes interannual variability inducing anticyclonic (cyclonic) Pacific Ocean circulation during El Niño (La Niña), and (4) high precipitation rates that occur in the Cabo Corrientes region during summer (Lavín et al. 2006, Godínez et al. 2010, Martínez-Flores et al. 2011). The Cabo Corrientes region is also influenced by a shallow oxygen minimum zone (<40 m depth, < 1 ml O₂ l⁻¹) characterizing the Tropical Surface Water (<30 m; also known as Equatorial Surface Water) with relatively high temperature (≥18°C) and low salinity (<34.9), and the Subtropical Subsurface Water with low temperature (≤18°C) and high salinity (Wyrski 1967, Filonov & Tereshchenko 2000, Cepeda-Morales et al. 2009).

In the Cabo Corrientes region, a conspicuous seasonal hydrographic cycle prevails that influences phytoplankton biomass and plankton community

structure. During the intense upwelling period (February to May), high chl *a* concentrations and primary productivity rates typically predominate, followed by a transitional upwelling relaxation period (June) and water column stratified conditions (July to December) when the lowest chl *a* concentrations and primary productivity rates typically occur (López Sandoval et al. 2009a,b).

Upwelling–downwelling pulses should play a significant role in the near-shore hydrographic conditions, plankton abundance, and community structure off Cabo Corrientes, as has been observed in highly productive temperate and transitional coastal wind-induced upwelling regions (Huyer 1983, Dorman et al. 2005, Gómez-Gutiérrez et al. 2005, Keister et al. 2005, 2009). A systematic zooplankton time series (December 1995 to December 1998) carried out in the Mexican central Pacific documented the effect of coastal upwelling events on zooplankton biomass and ichthyoplankton assemblage structure (Franco-Gordo et al. 2002, 2004). Previous krill studies in the ETP have been realized from single oceanographic cruises (Brinton 1979, Färber-Lorda et al. 1994, 2010, Gómez-Gutiérrez & Hernández-Trujillo 1994). Relatively more extensive studies about euphausiid biology and ecology have been performed on both sides of the Baja California peninsula (Brinton 1962, 1981, Brinton & Townsend 1980, 2003, Brinton et al. 1986, Lavaniegos 1994, Gómez-Gutiérrez et al. 1995, Lavaniegos & Ambriz-Arreola in press).

We studied tropical krill because it is relatively unknown whether their abundance is important to the regional pelagic food web and because the tropical zoogeographic component of zooplankton distributed in Mexican waters has been historically less studied than the west coast of Baja California and the Gulf of California, where temperate and subtropical krill fauna are distributed (Fernández-Álamo & Färber-Lorda 2006, Gómez-Gutiérrez et al. 2009). *Euphausia lamelligera* is the numerically dominant krill species in the tropical coastal habitat, and typically *E. eximia*, *E. distinguenda*, and *E. tenera* are the dominant krill species offshore (Färber-Lorda et al. 2010). Adults of these tropical euphausiids are opportunistic omnivores, able to switch diet type in response to changing trophic conditions, while larval stages feed on phytoplankton and microzooplankton (Mauchline & Fisher 1969). The depth of the oxygen minimum zone shapes the euphausiid daily vertical distribution and their zoogeographic affinities in the ETP region (Brinton 1979). Only 5 oceanographic surveys have been carried out in the mouth of the Gulf of California (including Cabo Corrientes) to

study euphausiid distribution, abundance, and community structure (Brinton 1962, 1979, Sánchez-Osuna & Hendrickx 1983, Gómez-Gutiérrez & Hernández-Trujillo 1994, Färber-Lorda et al. 2010). Thus, the seasonal and interannual changes in tropical euphausiid abundance and community structure are so far unknown. A zooplankton time series is likely the best sampling strategy to understand the effect of upwelling–downwelling dynamics and other oceanographic and climatic events influencing euphausiids and other zooplankton taxa. However, it is currently recognized that few time series are available for tropical ecosystems (Mackas & Beaugrand 2010). Multiple zooplankton time series have documented phenology, seasonal, interannual, and long-term environmental effects on the euphausiid community structure from Canada (49°N: Mackas et al. 2001, Mackas & Galbraith 2002), Oregon, USA (45°N: Peterson et al. 2002, Feinberg & Peterson 2003, Gómez-Gutiérrez et al. 2005, Keister et al. 2005), Monterey Bay, California, USA (36°N: Marinovic et al. 2002, Dorman et al. 2005), and California to the Baja California region (38–26°N: Brinton 1981, Brinton & Townsend 2003). Färber-Lorda et al. (2010) recognized the need for a seasonal study of euphausiid distribution and abundance to elucidate the mechanisms controlling their populations in this tropical ecosystem.

Here we reanalyzed monthly samples from a 1996 to 1998 time series of zooplankton samples, originally collected for a zooplankton biomass and ichthyoplankton study (Franco-Gordo et al. 2002, 2004), in order to investigate the effect of environmental conditions on tropical euphausiid abundance and community structure along the inshore Mexican central Pacific (southern Cabo Corrientes region, 19°N, 105°W). We propose that seasonal upwelling processes induce relatively high biomass and productivity in the tropical Cabo Corrientes ecosystem, as has been documented in transitional and temperate ecosystems. The goals of this study were (1) to test the hypothesis that abundance of tropical plankton (phytoplankton assemblages) and euphausiid abundance and community structure are strongly associated with variability in coastal upwelling intensity at a seasonal time scale in the southern Cabo Corrientes region, and (2) to investigate the response of the tropical euphausiid community to a strong, but relatively brief, El Niño event that occurred during 1997–98. Thus, this study will provide an initial baseline on the effect of seasonal environmental conditions and interannual variability imposed by an El Niño event on tropical euphausiid species.

MATERIALS AND METHODS

Study area and sample collection

Six oceanographic stations, located along the coasts of Jalisco and Colima states, Mexico (19°N, 105°W), were sampled approximately every month between January 1996 and December 1998 (Fig. 1). Oceanographic stations were 3 km apart and located <5 km from the coast where the seafloor depth was between 100 and 130 m. Standard conductivity, temperature, and depth (CTD, Seabird SB09) measurements were made ~10 m above the seafloor. Seawater samples were collected at 10 m depth every month during 1998 only, using 5 l Niskin bottles to record phytoplankton cell abundance and taxonomic composition.

In total, 146 zooplankton samples were collected during 26 oceanographic cruises using a standard Bongo net (61 cm diameter, 505 µm mesh) towed obliquely at 0.4 to 0.5 m s⁻¹ from 10 m above the sea bottom at shallow stations to the surface. Calibrated digital flowmeters installed in the mouth of each net were used to calculate the filtered seawater volume (Smith & Richardson 1977). All the zooplankton samples were preserved in 4% formalin saturated with sodium borate. The 1996–98 time series had several gaps in oceanographic cruises caused by climatic (hurricane season) or other logistical problems (August, September 1996; April, May, June, October,

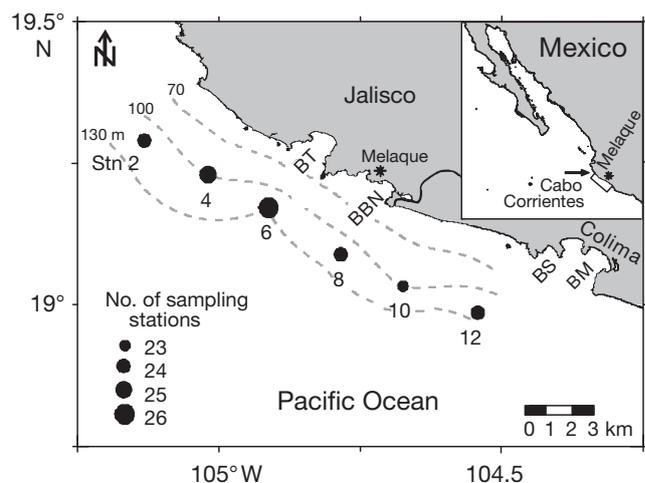


Fig. 1. Study area located along the southwest coast off Cabo Corrientes, showing the nighttime sampling stations located along the coast of Jalisco and Colima, Mexico. Circle sizes are proportional to the number of oceanographic stations sampled between January 1996 and December 1998. BT: Bahía Tenacatita, BBN: Bahía Barra de Navidad, BS: Bahía Santiago, BM: Bahía Manzanillo

November 1997; and February, October, November 1998). All zooplankton samples were collected at night (20:00 to 07:00 h) on board the RV 'BIP-V', owned by the Universidad de Guadalajara.

Laboratory analysis

Each 5 ml phytoplankton sample collected at 10 m depth was sedimented for >24 h to identify and count phytoplankton species using an inverted phase-contrast microscope using the standard Utermöhl technique (Hasle 1978). Nano- and microphytoplankton, consisting mainly of diatoms and dinoflagellates >5 µm, were identified using several taxonomic keys (Cupp 1943, Sournia 1967, Saunders & Glenn 1969, Steidinger & Williams 1970, Licea-Durán 1974, Taylor 1976, Pesantes 1978, Sournia et al. 1979), and their abundances were standardized (cells 1000 ml⁻¹).

Euphausiid species were separated from the samples, counted, and identified following standard taxonomic keys (Brinton 1996, Brinton et al. 2000). Most of the adult euphausiids were counted and identified from the complete zooplankton sample, while larvae (calyptopis and furcilia) and juveniles were separated and identified to species level from one-half, one-quarter, or one-eighth aliquots of the original sample. Euphausiid abundance was standardized to ind. 1000 m⁻³. At least 30 adults from the 2 most abundant species (*Euphausia distinguenda* and *E. lamelligera*) collected from each oceanographic station were selected for morphometric measurements. In total, 1063 specimens of *E. distinguenda* and 503 of *E. lamelligera* were sexed and measured for total length (TL, from the forward rim of the carapace to the distal end of the telson), carapace length (CL, from the base forward rim of the carapace to the posterior notch of the carapace), and the length of the hepatopancreas (HL, the longest length from the anterior to the posterior part of the hepatopancreas), also known as the digestive gland. The hepato-somatic index (HSI), defined as the ratio of HL to CL, is a valuable proxy to infer health and recent trophic conditions. We assumed that a small HSI indicates unfavorable feeding conditions and a large HSI indicates relatively favorable feeding conditions at a seasonal time scale (Shin 2000, Nicol et al. 2004, Virtue et al. 2010, O'Brien et al. 2011). All morphometric measurements were made with a calibrated ocular micrometer of a Carl Zeiss Discovery stereomicroscope (precision = 0.1 mm).

Data analysis

The biological variables analyzed were abundance of phytoplankton (cells l⁻¹) and euphausiid species (larvae and postlarvae, ind. 1000 m⁻³). Phytoplankton and euphausiid abundance were explored to detect outliers and later log transformed (log₁₀ [x+1]) for statistical analysis (see Fig. 3). A 1-way analysis of variance (ANOVA) was done to test whether significant differences exist in phytoplankton and euphausiid abundances among climatic periods defined during our study: semi-mixed (transitional), mixed (upwelling), and stratified (downwelling). A similar 1-way ANOVA was performed using the euphausiid HSI to detect differences among the same environmental condition periods. If an ANOVA was significant ($\alpha < 0.05$) for any of the variables tested, a Tukey's post hoc test was carried out to define the specific sampling unit that was significantly distinct from the others. Simple linear regression was used to test the relationship between HL and CL in *Euphausia distinguenda* and *E. lamelligera*, and the slopes were compared using analysis of covariance (ANCOVA; Zar 1996). All statistical analyses were conducted using Statistica 7.0 software (Stat Soft).

Canonical ordination methods were used to explore multivariate associations of phytoplankton and euphausiid species abundance (per development phase; calyptopis, furcilia, and juveniles + adults) with 9 environmental variables (see Table 5).

Monthly values of the multivariate ENSO index (MEI) and Southern Oscillation index (SOI) (www.esrl.noaa.gov/psd/enso/mei/) were used as proxies to detect the duration and intensity of the 1997–98 El Niño event in the area of study. The daily coastal upwelling index (CUI, m³ s⁻¹ per 100 m coastline; Bakun 1973), calculated from the location 21° N, 107° W, was used to explore the temporal variability of coastal upwelling–downwelling conditions on the day of zooplankton sampling as well as 8 and 15 d before each sampling event (www.pfel.noaa.gov/products/products.html). The mixed layer depth (MLD) was estimated as the depth at which the temperature was 1°C lower than the temperature at the 10 m layer. To obtain a proxy of water column stability, a thermal stratification index (TSI) was estimated as the difference between temperature at 10 and 90 m depth (maximum depth of CTD casts) at each oceanographic station. The monthly anomaly values of TSI were calculated as:

$$Z_{ij} = X_{ij} - Y_i \quad (1)$$

where Z_{ij} is the TSI anomaly of the j^{th} month in the i^{th} year, X_{ij} is the TSI value in the j^{th} month in the i^{th}

year, and Y_i is the mean TSI value in the i^{th} month for the 3 yr.

Multivariate statistical analysis was performed using 2 matrices: one with euphausiid abundance per species (columns) and oceanographic stations (rows) and the other with all of the environmental variables (columns) and oceanographic stations (rows; see Table 5). Because *Euphausia eximia*, *E. diomedae*, *E. tenera*, *Stylocheiron affine*, and *S. carinatum* were detected only in <5% of the zooplankton samples, these species were excluded in the multivariate statistical analysis. Thus, the euphausiid species matrix (7 columns \times 135 rows) included the 3 most abundant krill species (*E. distinguenda*, *E. lamelligera*, and *Nematoscelis gracilis*) by development phase (larvae and postlarvae) and total euphausiid abundance. To select the most robust canonical analysis, a detrended correspondence analysis of the euphausiid species matrix was used to obtain the length of the environmental gradients (ter Braak & Prentice 2004). This methodology was also used for the dominant phytoplankton taxa matrix collected during 1998 (30 columns \times 43 rows). These gradients were 1.61 for the first axis and <1.5 for the rest of the euphausiid matrix axes, and 1.88 for first axis and <1.2 for the rest of the phytoplankton matrix axes. We used a linear response model for both matrices. Species–environment relationships were explored using redundancy analysis (RDA; Legendre & Legendre 1998). For these statistical analyses, scaling was focused on the interspecies euphausiid correlations. Species scores were divided by their correspondent standard deviation and centered by euphausiid species. Forward selection of environmental variables was performed automatically, and statistical significance was calculated using unrestricted Monte Carlo permutation tests.

Environmental matrices of phytoplankton recorded during 1998 (7 columns \times 43 rows), and euphausiids recorded during 1996 to 1998 (9 columns \times 135 rows) were used for the RDA. Tri-plots were used for the representation of the biological variables ordination in the environmental multi-dimensional space (Legendre & Legendre 1998). All statistical multivariate analyses were performed with the CANOCO software ver. 4.5 (ter Braak & Šmilauer 2002).

RESULTS

Oceanographic conditions

The oceanographic conditions of the 1997–98 El Niño event were first detected in the Cabo Corri-

entes region with MEI and SOI proxies in May 1997, and these atmospheric and oceanographic conditions prevailed until June 1998 (Fig. 2A). The daily CUI ($\text{m}^3 \text{s}^{-1}$ per 100 m coastline, estimated for the 21° N, 107° W location) showed continuous low-intensity upwelling events between December 1996 and June 1997 and relatively short periods of pronounced downwelling events between July and November of each year (1996–1998; Fig. 2B). Considerable inter-annual variability was observed, and although the number of days with upwelling events (positive values $>1 \text{ CUI m}^3 \text{ s}^{-1}$ per 100 m coastline) was similar among years (86, 79, and 81% for 1996, 1997, and 1998, respectively), upwelling intensity ($>100 \text{ CUI m}^3 \text{ s}^{-1}$ per 100 m coastline) was significantly higher during 1998 than during 1996 and 1997 ($F = 13.63$, $p < 0.001$; Fig. 2B). The number of days with downwelling events (negative values for CUI) was slightly greater during 1997 (20%) and 1998 (18%) than during 1996 (12%), but intensity did not show significant statistical differences.

Vertical distribution of temperature and salinity recorded in the upper 100 m of the water column also showed clear interannual changes. The MLD was shallow during May to October 1996 (~24 m), deepening further from the second semester of 1997 to early 1998 (60–80 m), and moderately deep from May to September 1998 (40 m; Fig. 2C). Salinity was typically homogeneous throughout the year (salinities >34.3), but short periods with low near-surface salinities were associated with the regional hurricane season (July to August; Fig. 2D).

The vertical thermohaline structure also had a strong seasonal pattern (Fig. 2C,D). The temperature from January to May ranged between 14 and 22°C with a typical mixed water column, probably associated with intense coastal upwelling activity (Fig. 2B). Episodic downwelling periods occurred between July and October when upwelling events were considerably less intense and temperature ranged between 14 and 31°C (Fig. 2B–D).

In 1996, 3 distinct periods for the TSI were distinguished: (1) a period of mixed water column (M) with low average thermal stratification values (7 to 10°C), that typically occurred from February to May; (2) a stratified period (S) with higher temperatures ($>14^\circ\text{C}$), and positive temperature ($>2^\circ\text{C}$) and salinity anomalies, typically occurring from June to November; and (3) a semi-mixed transitional period (SM) that typically occurred between June and December/January (Fig. 3A,B). During the 1997–98 El Niño event, 3 phases were also detected, which in order of sequence were: El Niño semi-mixed

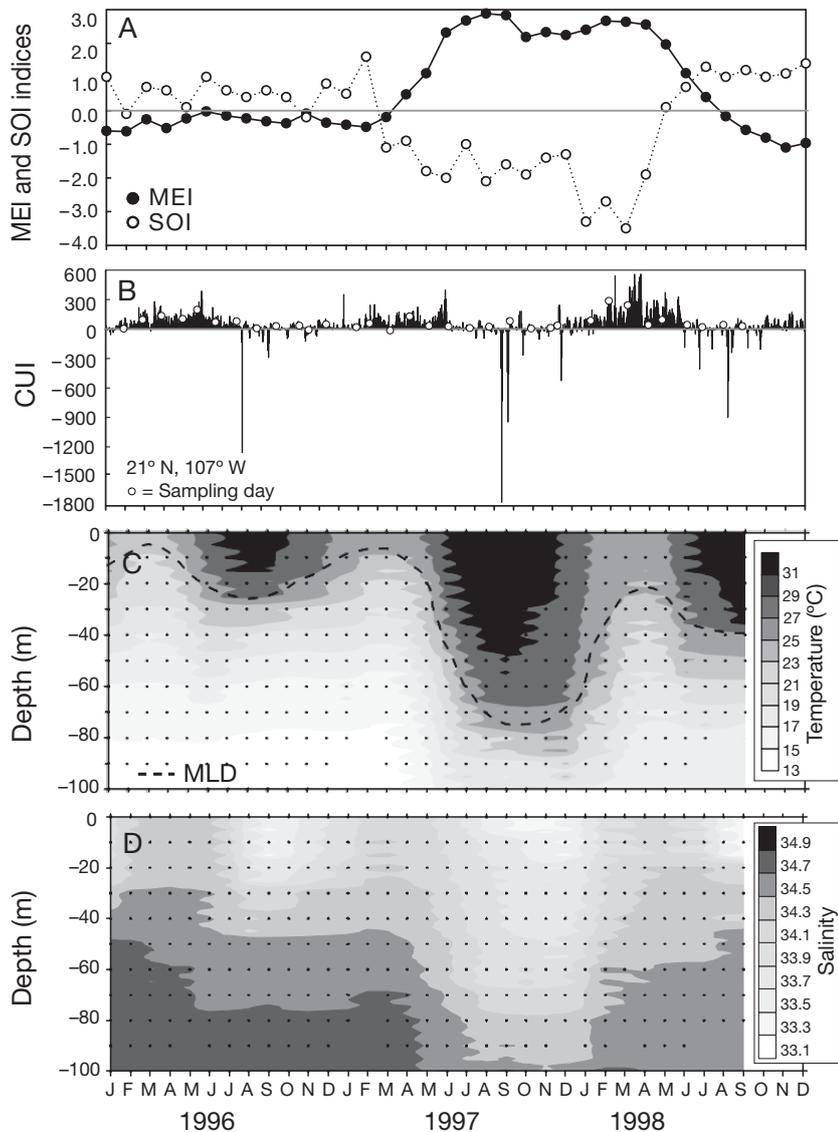


Fig. 2. Time series of environmental and oceanographic conditions recorded during 1996 to 1998 in the Cabo Corrientes region. (A) Multivariate El Niño Southern Oscillation (ENSO) index (MEI) and Southern Oscillation index (SOI) obtained from the US National Oceanic and Atmospheric Administration (NOAA; www.esrl.noaa.gov/psd/data/climateindices/list/). (B) Daily coastal upwelling index (CUI, $\text{m}^3 \text{s}^{-1}$ per 100 m coastline, 21°N , 107°W ; NOAA). (C) Temperature. (D) Salinity. Data in (C) and (D) are the mean values of 6 oceanographic stations sampled along the coast of Jalisco and Colima, Mexico

(ENSM), El Niño mixed (ENM), and El Niño stratified (ENS) periods. These 3 periods were temporally associated, respectively, with intense upwelling (M), upwelling relaxation (SM), and downwelling (S) periods. A Kruskal-Wallis test indicated that the TSI values of the 3 periods significantly differed from each other ($H = 54.41$, $p < 0.0001$), which further supported the M, SM, and S classification periods (Fig. 3A,B).

Seasonal variability of phytoplankton during 1998

The nano- and microphytoplankton abundances counted from 6 oceanographic stations during 1998 showed 2 significantly distinct seasonal periods (Fig. 4A,B). Diatom abundance was significantly higher from March to May than during the rest of the year ($F = 14.442$, $p < 0.001$). However, diatom abundance increased moderately during September and December (Fig. 4A). In contrast, dinoflagellates had significantly lower abundances during the M period than during the S water column period ($F = 11.469$, $p < 0.001$).

During the 1998 phytoplankton sampling period, 52 nano- and microphytoplankton taxa were identified, including a group of 6 unidentified taxa. Most of the phytoplankton species identified were diatoms from 17 genera (87%; Table 1). The most common phytoplankton genera were *Chaetoceros* (10 species), *Rhizosolenia* (9 species), and *Nitzschia* (3 species). Thirty species of the genera *Rhizosolenia*, *Chaetoceros*, *Nitzschia*, *Leptocylindrus*, *Ditylum*, *Thalassiothrix*, and *Protoperdinium* contributed >98% of the phytoplankton abundance from the Cabo Corrientes region. Mean cell abundances of 16 diatom species showed significant differences among periods of thermal conditions (Table 1), as did the 6 dominant genera combined ($F = 10.690$, $p < 0.001$). Tukey's test indicated that the mean abundance of *Rhizosolenia*, *Chaetoceros*, *Nitzschia*, and *Leptocylindrus* tended to increase during the M period (with intense upwelling events), and mean cell density

decreased during SM and S periods ($F = >9.590$, $p < 0.001$ in all cases). Twelve phytoplankton species had significantly higher abundances during the M period than during the rest of the year. The most abundant phytoplankton species (*C. curvisetus*, *L. danicus*, and *R. stolterforthii*) had their peaks of abundance in March, April, and May (M period), drastically decreasing their abundance during the S and SM periods (Table 1). The diatoms *D. brightwellii* and *T.*

Fig. 3. Thermal stratification index (TSI) from January 1996 to December 1998 on the Jalisco and Colima continental shelf. (A) Monthly means ($\pm 95\%$ confidence intervals); (B) monthly anomaly of TSI after removing the monthly long-term means. Conditions of the water column are indicated as SM: semi-mixed period; M: mixed period; S: stratified period. Periods under the influence of El Niño are ENSM: El Niño semi-mixed; ENM: El Niño mixed; and ENS: El Niño stratified conditions

fravenfeldii, along with 4 other species, showed a significant increase in abundance during the S and SM periods. The dinoflagellate genus *Proto-peridinium* was absent during the M period (Table 1) and exhibited considerably high abundance during the SM and S periods ($F = 28.85$; $p < 0.05$).

Seasonal/interannual variability in euphausiid abundance and community composition

Eight euphausiid species, belonging to 3 genera, were identified during the 1996 to 1998 time series (Table 2). Euphausiid abundance was pooled into 3 developmental phases: (1) calyptopis larvae, (2) furcilia larvae, and (3) postlarvae (juveniles + adults). Euphausiid richness per oceanographic station was typically < 3 species, except during the El Niño event (May 1997 to June 1998) when up to 5 species were recorded at the same oceanographic station due to the presence of oceanic species (*E. diomedae*, *E. tenera*, *Stylocheiron affine*, *S. carinatum*, and *Nematoscelis gracilis*; Fig. 5A).

Euphausia distinguenda and *E. lamelligera* were the most abundant euphausiid species during the 3 yr, contributing $> 97.9\%$ of the euphausiid abundance in any development phase (Fig. 5B–D). *E. distinguenda* accounted for 87.8 to 89.5% of the total euphausiid abundance, having higher postlarval abundance (juveniles + adults) during periods with intense upwelling. High calyptopis and furcilia abundances were consistently associated with SM periods and

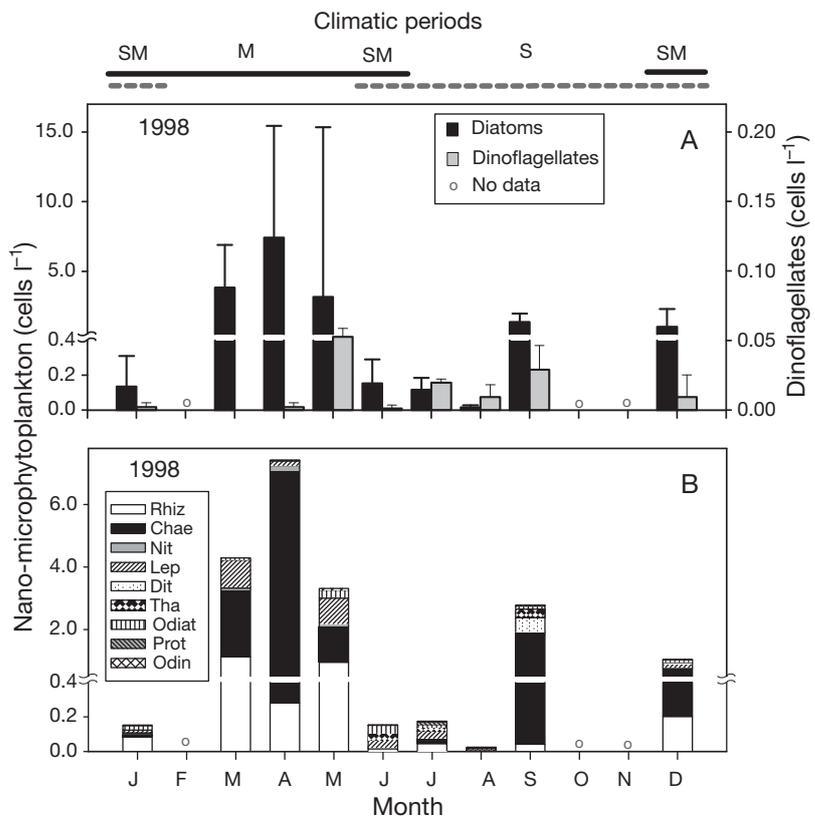
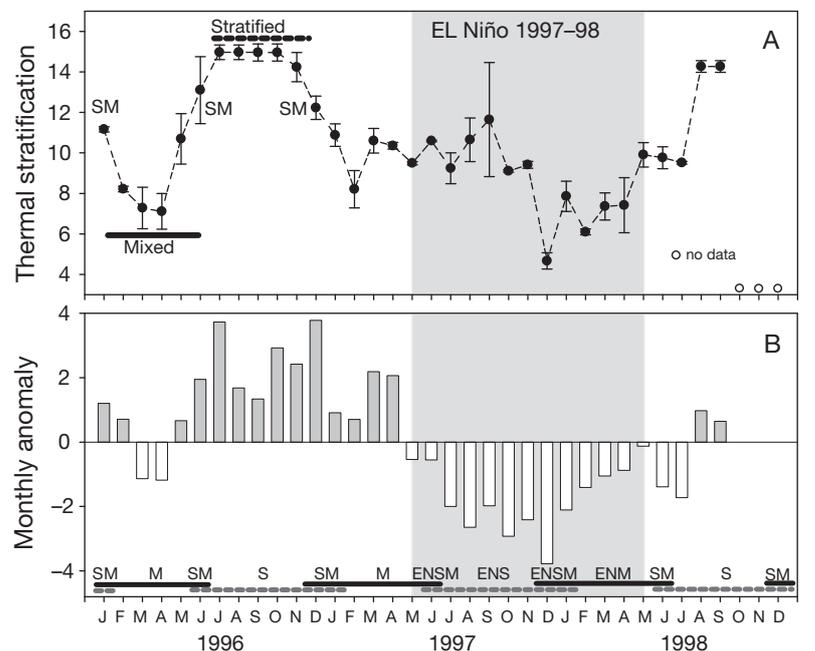


Fig. 4. Monthly mean ($\pm 95\%$ confidence interval) of phytoplankton abundance from 10 m depth detected during 1998: (A) diatoms and dinoflagellates, (B) dominant genera *Rhizosolenia* (Rhiz), *Chaetoceros* (Chae), *Nitzschia* (Nit), *Leptocylindrus* (Lep), *Ditylum* (Dit), *Thalassiothrix* (Tha), other diatoms (Odia), *Proto-peridinium* (Prot), and other dinoflagellates (Odin). SM, M, and S periods as defined in Fig. 3

Table 1. Mean and standard deviation (SD) of diatom and dinoflagellate cell abundance (cells l⁻¹) per oceanographic period during 1998 off the Cabo Corrientes region, Mexico. Only the most abundant phytoplankton species are shown (the rest of the species were pooled into 'other diatoms' or 'other dinoflagellates'). n indicates the frequency of the species, i.e. number of samples in which it was found out of the total number of samples analyzed during each period (15, 15, and 17 for SM, M, and S periods, respectively, as defined in Fig. 3). ANOVA (*F*, *p*) comparisons among periods with significant results ($\alpha = 0.05$) are shown in **bold**. Environmental condition abbreviations are as defined in Fig. 3

Species	Code	Semi-mixed (SM) Mean ± SD (n)	Mixed (M) Mean ± SD (n)	Stratified (S) Mean ± SD (n)	<i>F</i>	<i>p</i>
Diatoms						
<i>Chaetoceros atlanticus</i>	Ctla	11.5 ± 28.0 (4)	30.0 ± 46.4 (8)	– (0)	10.383	<0.001
<i>C. affinis</i>	Caff	15.7 ± 46.5 (3)	125.5 ± 248.3 (11)	13.9 ± 20.0 (7)	9.234	<0.001
<i>C. brevis</i>	Cbre	– (0)	5.1 ± 19.6 (1)	– (0)	0.930	0.403
<i>C. costatus</i>	Ccos	103.0 ± 231.5 (3)	116.8 ± 159.6 (9)	109.3 ± 169.2 (7)	5.137	0.010
<i>C. curvisetus</i>	Ccur	89.2 ± 218.4 (3)	3464.9 ± 5452.9 (11)	51.7 ± 114.8 (6)	14.261	<0.001
<i>C. danicum</i>	Cdan	– (0)	3.2 ± 12.4 (1)	– (0)	0.930	0.403
<i>C. difficilis</i>	Cdif	0.9 ± 3.4 (1)	– (0)	– (0)	1.488	0.238
<i>C. didymus</i>	Cdid	– (0)	– (0)	4.5 ± 8.9 (4)	3.679	0.034
<i>C. messanense</i>	Cmas	– (0)	– (0)	0.4 ± 1.7 (1)	0.756	0.476
<i>C. pelagicus</i>	Cpel	– (0)	4.6 ± 17.8 (1)	– (0)	0.930	0.403
<i>Chaetoceros</i> spp.	Cspp	1.9 ± 7.2 (1)	– (0)	– (0)	1.488	0.238
<i>Ditylum brightwellii</i>	Dbri	17.1 ± 36.0 (4)	4.9 ± 11.0 (4)	158.6 ± 285.6 (6)	3.918	0.028
<i>Leptocylindrus danicus</i>	Ldan	62.8 ± 117.1 (8)	568.1 ± 617.2 (13)	2.5 ± 4.2 (5)	21.943	<0.001
<i>Nitzschia delicatissima</i>	Ndel	6.1 ± 12.7 (3)	84.5 ± 78.5 (12)	8.2 ± 21.2 (4)	11.650	<0.001
<i>N. longissima</i>	Nlon	6.9 ± 25.0 (2)	– (0)	– (0)	1.488	0.238
<i>N. pacifica</i>	Npac	9.7 ± 25.7 (3)	36.4 ± 39.1 (12)	3.6 ± 10.9 (2)	21.513	<0.001
<i>Rhizosolenia alata</i>	Rala	4.7 ± 9.0 (4)	6.0 ± 23.2 (1)	0.4 ± 1.7 (1)	0.189	0.829
<i>R. bergonii</i>	Rber	2.8 ± 7.8 (2)	– (0)	5.4 ± 7.2 (8)	10.108	<0.001
<i>R. calcar avis</i>	Rcal	4.1 ± 16.0 (1)	8.8 ± 27.3 (2)	– (0)	1.087	0.347
<i>R. delicatula</i>	Rdel	2.3 ± 5.0 (3)	2.3 ± 6.2 (2)	– (0)	1.309	0.281
<i>R. fragilissima</i>	Rfra	2.3 ± 9.0 (1)	71.5 ± 95.7 (8)	0.8 ± 3.4 (1)	8.943	<0.001
<i>R. hebetata</i>	Rheb	– (0)	– (0)	2.1 ± 4.1 (4)	3.650	0.035
<i>R. setigera</i>	Rset	1.3 ± 3.6 (2)	24.3 ± 37.4 (8)	3.7 ± 5.6 (6)	3.437	0.042
<i>R. stouterforthii</i>	Rsto	102.1 ± 176.8 (9)	480.3 ± 627.6 (13)	18.8 ± 33.2 (6)	12.067	<0.001
<i>R. styliformis</i>	Rsty	1.3 ± 3.6 (2)	24.6 ± 34.5 (10)	– (0)	14.972	<0.001
<i>Thalassiothrix frauenfeldii</i>	Tfra	22.7 ± 42.4 (5)	6.0 ± 13.0 (3)	102.7 ± 147.6 (10)	4.870	0.013
Other diatoms ^a	Odiat	43.8 ± 54.5 (12)	73.1 ± 101.4 (13)	35.5 ± 56.9 (12)	0.902	0.413
Dinoflagellates						
<i>Protoperidinium</i> spp.	P spp	0.9 ± 3.6 (1)	– (0)	15.9 ± 14.2 (14)	42.547	<0.001
Other dinoflagellates ^b	O din	3.8 ± 8.8 (5)	11.3 ± 40.6 (3)	4.9 ± 5.9 (8)	1.052	0.359

^a*Asterionella japonica*, *Biddulphia alternatus*, *B. cf. alternans*, *B. longicuris*, *B. mobilensis*, *Ceratulina bergonii*, *Coscinodiscus centralis*, *Coscinodiscus lineatus*, *Coscinodiscus* spp., *Hemialus sinensis*, *Navicula* spp., *Planktoniella sol*, *Pleurosigma* spp., *Prorocentrum gracile*, *Prorocentrum micans*, *Protoperidinium* spp., *Schröderella delicatula*, *Streptotheca thamesis*

^b*Ceratium furca*, *Ceratium massilense*, *Ceratium* sp., *Ceratium trichoceros*, *Ceratium tripos*, *Prorocentrum gracile*, *Prorocentrum micans*, *Prorocentrum* sp.

with the 1997–98 El Niño. *E. lamelligera* larvae and postlarvae accounted for 8.4 to 11.9% of the euphausiid abundance, with higher densities detected during mixed conditions. The rest of the euphausiid species occurred at low abundances (<2.3%), but *E. tenera* and *Nematoscelis gracilis* were collected at high relative abundances during El Niño winter (December 1997 and January 1998).

Euphausiid abundance and species composition showed considerable seasonal and interannual variability throughout the time series (Fig. 5B–D, Tables 2 & 3). A post hoc Tukey's test of multiple comparisons

revealed that postlarvae total abundance (mainly *Euphausia distinguenda* and *E. lamelligera*) were significantly higher during M periods (geometric means ranged from 1640 to 2430 ind. 1000 m⁻³) than during SM (280 to 1480 ind. 1000 m⁻³) and S periods (270 to 740 ind. 1000 m⁻³). Abundance of oceanic postlarvae (mostly *E. tenera* and *Nematoscelis gracilis*) significantly increased during El Niño conditions compared to the rest of the period studied (Tukey's test *p* < 0.05, Table 3).

A relatively high percentage of furciliae from 5 oceanic species (*Euphausia diomedea*, *E. tenera*,

Table 2. Geometric mean abundance of euphausiids (ind. 1000 m⁻³) per developmental stage: calyptopis, furcilia, and postlarvae (juveniles + adults) during periods with distinct environmental conditions recorded during 1996 to 1998. n = frequency of the species, i.e. number of samples in which it was found out of the total zooplankton samples analyzed in each period (30, 31, 33, 18, 16, and 18 for periods SM, M, S, ENSM, ENM, and ENS, respectively; periods as defined in Fig 3). Euphausiid abundance data were log transformed before the calculation of the mean, and then back-transformed to obtain the geometric mean. ANOVA (*F*, *p*) with significant results are shown in **bold** ($\alpha = 0.05$)

Species	SM Mean (n)	M Mean (n)	S Mean (n)	ENSM Mean (n)	ENM Mean (n)	ENS Mean (n)	<i>F</i>	<i>p</i>	<i>A posteriori</i> contrast (Tukey's test)
Calyptopis									
<i>Euphausia distinguenda</i>	4.6 (10)	3.0 (7)	5.0 (12)	17.4 (11)	6.5 (5)	2.1 (6)	0.96	0.23	
<i>E. lamelligera</i>	1.7 (6)	0.4 (2)	0.3 (2)	0.3 (2)	0.6 (1)	0.0 (0)	1.52	0.187	
<i>E. tenera</i>	0.0 (0)	0.0 (0)	0.0 (0)	0.5 (2)	0.0 (0)	0.0 (0)	2.71	0.023	ENSM>All
Furcilia									
<i>E. distinguenda</i>	139.0 (27)	17.8 (17)	241.2 (27)	101.7 (14)	23.3 (9)	15.3 (10)	4.06	<0.001	S>M, S>ENS
<i>E. lamelligera</i>	11.8 (12)	18.2 (19)	2.8 (8)	6.6 (7)	1.9 (4)	1.2 (3)	2.39	0.041	
<i>Nematoscelis gracilis</i>	0.0 (0)	0.0 (0)	0.0 (0)	19.9 (11)	0.8 (2)	0.0 (0)	26.09	<0.001	ENSM>All
<i>E. diomedae</i>	0.0 (0)	0.2 (2)	0.3 (2)	0.0 (0)	1.1 (3)	1.1 (3)	2.07	0.073	
<i>E. tenera</i>	0.2 (2)	0.4 (2)	0.4 (2)	7.8 (8)	0.0 (0)	0.0 (0)	6.98	<0.001	ENSM>All
<i>E. eximia</i>	0.0 (0)	0.1 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.73	0.600	
<i>Stylocheiron affine</i>	0.0 (0)	0.0 (0)	0.1 (1)	0.2 (1)	0.4 (2)	0.0 (0)	1.34	0.252	
<i>S. carinatum</i>	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.4 (1)	0.2 (1)	1.50	0.193	
Postlarva									
<i>E. distinguenda</i>	735.6 (29)	512.8 (29)	155.9 (27)	167.6 (16)	1006.2 (14)	93.0 (12)	3.25	<0.001	
<i>E. lamelligera</i>	58.7 (19)	256.2 (25)	6.1 (12)	9.2 (9)	216.6 (12)	41.2 (11)	5.81	<0.001	M>S, M>ENSM, ENM>S
<i>N. gracilis</i>	0.1 (1)	0.0 (0)	0.0 (0)	13.1 (12)	0.0 (0)	0.0 (0)	37.15	<0.001	ENSM>All
<i>E. diomedae</i>	0.2 (2)	0.1 (1)	0.2 (2)	0.0 (0)	0.0 (0)	0.7 (2)	1.64	0.153	
<i>E. tenera</i>	0.0 (0)	0.0 (0)	0.2 (2)	0.6 (3)	0.0 (0)	0.0 (0)	2.52	0.033	ENSM>SM, ENSM>M
<i>E. eximia</i>	0.0 (0)	0.0 (0)	0.0 (0)	0.2 (1)	0.0 (0)	0.0 (0)	1.48	0.199	
<i>S. affine</i>	0.1 (1)	0.4 (3)	0.3 (3)	0.3 (1)	0.8 (2)	0.0 (0)	0.98	0.433	
<i>S. carinatum</i>	0.2 (1)	0.0 (0)	0.1 (1)	0.0 (0)	1.2 (2)	0.4 (2)	2.00	0.082	

Stylocheiron affine, *S. carinatum*, and *Nematoscelis gracilis*) invaded the neritic environment of the Cabo Corrientes region during the 1997–98 El Niño event (Table 3). With the re-establishment of typical oceanographic conditions during July 1998, the abundance of these 5 species decreased significantly ($p < 0.05$) or they were absent. A similar trend was observed with *N. gracilis* juvenile and adult abundance. In contrast, both calyptopis and furcilia phases of *E. lamelligera*, as well as total furciliae abundance, showed a significant decrease during the 1997–98 El Niño period (Table 3).

Phytoplankton and euphausiid species relationships with environmental conditions

The RDA of phytoplankton and euphausiid species as a function of the environmental conditions showed a clear separation of the M, S, and SM periods (Fig. 6). The 3 RDA canonical ordination axes explained 41.1% of the total variance for phytoplankton species in the multidimensional environmental space with significant correlation in axis 1 ($F = 14.19$, $p < 0.001$; and $F = 4.42$, $p < 0.001$ for

all axes). The species–environment relationship explained 88% of the total variance (Table 4). The first RDA axis showed the highest positive correlation with CUI and a negative correlation with 10 m depth temperature, MLD, and TSI prevailing during the M period (upwelling season). The first RDA axis had a strong positive correlation with 17 numerically dominant phytoplankton species, particularly with *Chaetoceros curvisetus*, *C. atlanticus*, *C. affinis*, *Lep- tocyllindrus danicus*, *Nitzschia delicatissima*, *N. paci- fica*, *Rhizosolenia stolterforthii*, *R. styliiformis*, and *R. fragilissima* (Table 1, Fig. 6A). The second axis was mainly associated with the TSI (Table 4). The CUI on the sampling day and CUI 8 d before sam- pling had a relatively weak and negative correlation with the second axis. All of these sample units were associated with the strong S period (downwelling season). *Ditylum brightwellii*, *Thalassiothrix frauen- feldii*, *C. didymus*, *R. bergonii*, *R. hebetata*, and *Proto- peridinium* spp. were strongly associated with the second axis environmental gradient (Fig. 6A, Table 1).

Three clusters of oceanographic stations were identified in the RDA plot of euphausiid species per development phase in the oceanographic stations space (Fig. 6B). Stations sampled during the M

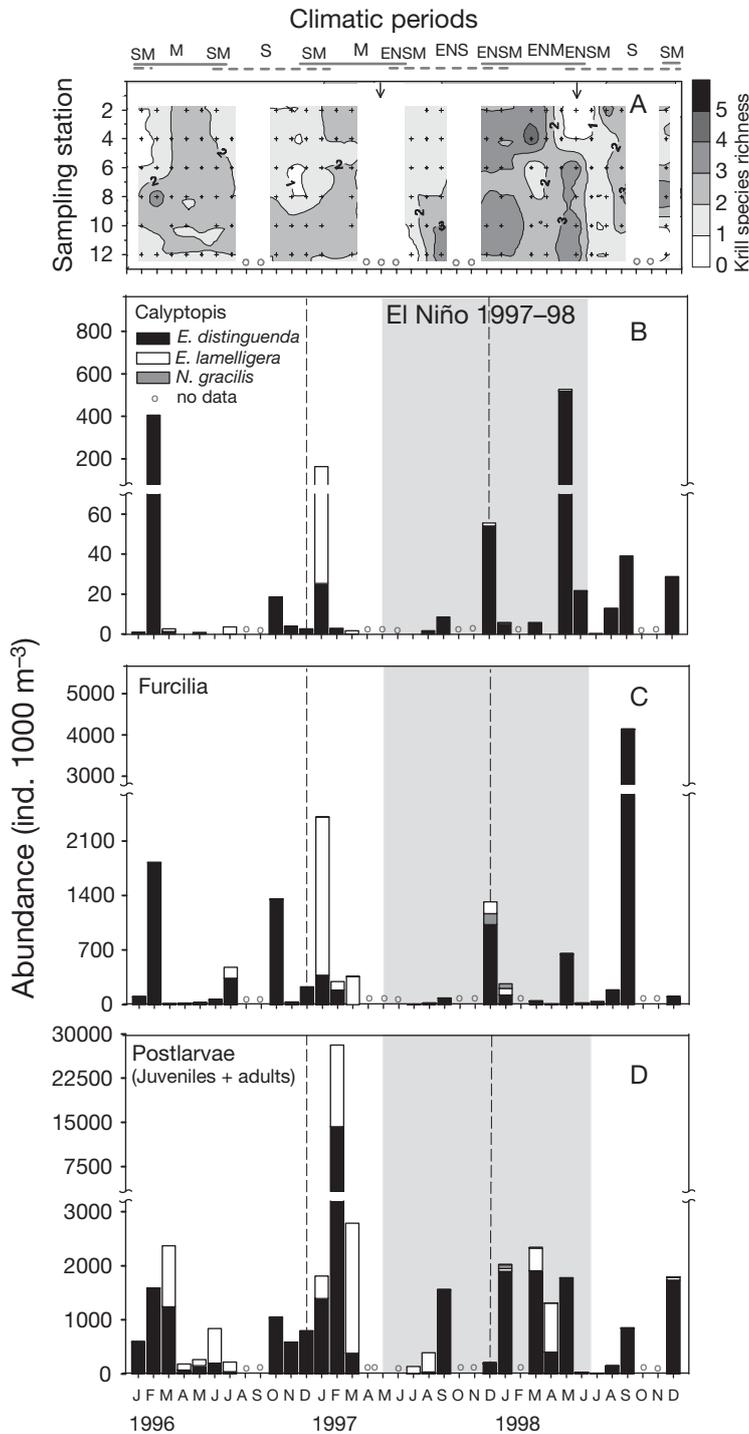


Fig. 5. Euphausiid species richness and abundance (ind. 1000 m⁻³) along the Jalisco and Colima coasts collected during 1996 to 1998: (A) monthly latitude changes of euphausiid species richness, (B–D) monthly geometric stacked abundance means of the 3 most abundant euphausiid species (*Euphausia distinguenda*, *E. lamelligera*, and *Nematoscelis gracilis*) per life phases: (B) calyptopis larvae, (C) furcilia larvae, and (D) postlarvae. The period under the influence of the 1997–98 El Niño event is delimited with arrows in (A) and the gray area in (C–D). SM, M, and S conditions as defined in Fig. 3

period were clustered mainly on the right side of horizontal axis 1, significantly associated with CUI at 8 d before the sampling date. Stations sampled during the short S periods were clustered mainly on the upper left side of this axis and positively associated with vectors of 10 m temperature and MLD. Central sampling stations represented those sampled during the SM period (semi-mixed water column). Euphausiid abundance was principally affected by seasonal variability in stratification conditions, being particularly abundant during the M period.

The first 2 RDA axes explained 25% of the total variance for euphausiid species abundance with significant correlation in axis 1 ($F = 21.06$, $p < 0.001$) and for all axes ($F = 5.99$, $p < 0.001$); while 83% of the variance was explained in the species–environment relationship (Table 5). The first RDA axis had high correlations with 10 m salinity, CUI (monthly), CUI at 15 d before sampling, and a negative correlation with 10 m temperature. Total euphausiid and *Euphausia distinguenda* and *E. lamelligera* postlarvae abundances were significantly correlated with the first axis environmental gradient. This result indicates that they had high abundance associated with low temperature, and relatively high salinity and phytoplankton cell abundance (Fig. 6B). The second axis explained 10.5% of species variability and 35% of the species–environment relationship, showing a positive correlation with temperature and a negative correlation with CUI at 8 d before sampling and also with CUI on the respective sampling day. Only *E. distinguenda* and *Nematoscelis gracilis* larvae were strongly associated with the second axis environmental gradient (Fig. 6B). The second axis gradient reflects oligotrophic conditions that prevailed during the S period and the tropical influence of El Niño.

Sex ratio, biometry, and HSI

The mean seasonal variability of adult *Euphausia distinguenda* and *E. lamelligera* sex ratio, TL, CL, and HSI showed different responses during each environmental period (Figs. 7 & 8). Mean sex ratio was close to 50% throughout most of the time series except during periods of mixed water column conditions

Table 4. Summary of the redundancy analysis (RDA) using 7 environmental variables and abundances of 30 phytoplankton species collected at 43 oceanographic stations sampled during 1998. Significant correlations ($\alpha = 0.05$) with each environmental variable and the RDA axes are indicated with asterisks. CUI: coastal upwelling index

Ordination axes	1	2	3
Eigenvalues	0.288	0.093	0.029
Species–environment correlations	0.862	0.699	0.737
Cumulative variance (%)			
Species	28.8	38.1	41.1
Species–environment relation	61.5	81.3	87.6
Inter-set correlations of environmental variables with species axes			
Thermal stratification	–0.561*	0.671*	–0.041
10 m temperature	–0.805*	0.244	–0.353
10 m salinity	0.203	0.365	0.093
Mixed layer depth	–0.704*	–0.270	–0.014
CUI (monthly)	0.809*	–0.268	0.224
CUI on sampling day	0.353	–0.475*	–0.326*
CUI 8 d before sampling	–0.062	–0.385*	–0.450*

DISCUSSION

We demonstrated that tropical euphausiid species inhabiting a coastal region of the ETP are sensitive to seasonal changes of upwelling–downwelling variability and interannual climatic–oceanographic perturbations (like El Niño) as are euphausiid species of higher latitudes distributed in subtropical and temperate ecosystems. Those changes were evident in: (1) euphausiid species composition, which was more diverse during the El Niño event with the invasion of oceanic species toward the neritic environment, (2) euphausiid abundance, which was greater during the upwelling season (M period) than during the transitional (SM period) and downwelling (S period) seasons, and (3) body condition and trophic status, indicated by the HSI, which was significantly higher during the M and SM periods than during the S period. Thus, a dynamic perspective emerges from the analysis of this relatively short time series in a tropical Mexican ecosystem that is, to our knowledge, one of the few multi-year systematic time series done in tropical latitudes (Mackas & Beaugrand 2010).

Changes in the oceanographic conditions and phytoplankton

The seasonal variability of the thermohaline vertical column water structure off the Cabo Corrientes

Table 5. Summary of the redundancy analysis (RDA) using 9 environmental variables and the abundances of the most abundant euphausiid species collected from 135 stations obtained during 1996 to 1998. Significant correlations ($\alpha = 0.05$) with each environmental variable and the RDA axes are indicated with asterisks. SOI: Southern Oscillation index, CUI: coastal upwelling index

Ordination axes	1	2	3
Eigenvalues	0.144	0.105	0.032
Species–environment correlations	0.63	0.584	0.762
Cumulative variance (%)			
Species	14.4	25	28.2
Species–environment relation	47.8	82.8	93.5
Inter-set correlations of environmental variables with species axes			
Thermal stratification	–0.266	0.019	–0.700*
10 m temperature	–0.478*	0.590*	0.002
10 m salinity	0.528*	0.100	–0.366
Mixed layer depth	–0.265	0.248	0.548*
SOI	–0.235	0.219	–0.647*
CUI (monthly)	0.547*	–0.285	0.287
CUI on sampling day	–0.027	–0.372*	0.506*
CUI 8 d before sampling	–0.202	–0.438*	0.010
CUI 15 d before sampling	0.479*	0.016	0.211

coastal region had a strong influence during the 1997–98 El Niño event (Fig. 2). On the seasonal time scale, we demonstrated that between February and early June, the upper water column (surface to 40 m depth) was considerably colder, saltier, mixed, and with a shallower MLD than during the rest of the year, indicating the influence of intense upwelling activity during this period (Figs. 2C,D & 3). López-Sandoval et al. (2009a,b) reported maximum surface chl *a* concentration ($>2 \text{ mg m}^{-3}$) and higher mean primary productivity rates ($447 \text{ mg C m}^{-2} \text{ d}^{-1}$) between February and June corresponding to M and SM periods off Cabo Corrientes. In the context of our results, it seems that the abundance of euphausiids in the Cabo Corrientes region is predominantly bottom-up controlled. Recent studies also have shown evidence of this bottom-up control in the Cabo Corrientes region in phytoplankton (Cepeda-Morales et al. 2009), ichthyoplankton (León-Chávez et al. 2010), and yellowfin tuna (Torres-Orozco et al. 2005).

The cessation of winds or decreasing wind intensity caused downwelling events that led to strong near-surface thermal stratification from early July to November and induced significant changes in phytoplankton and euphausiid abundance and species composition. During S periods, surface waters near the coast tended to deepen the thermocline ($>28 \text{ m}$)

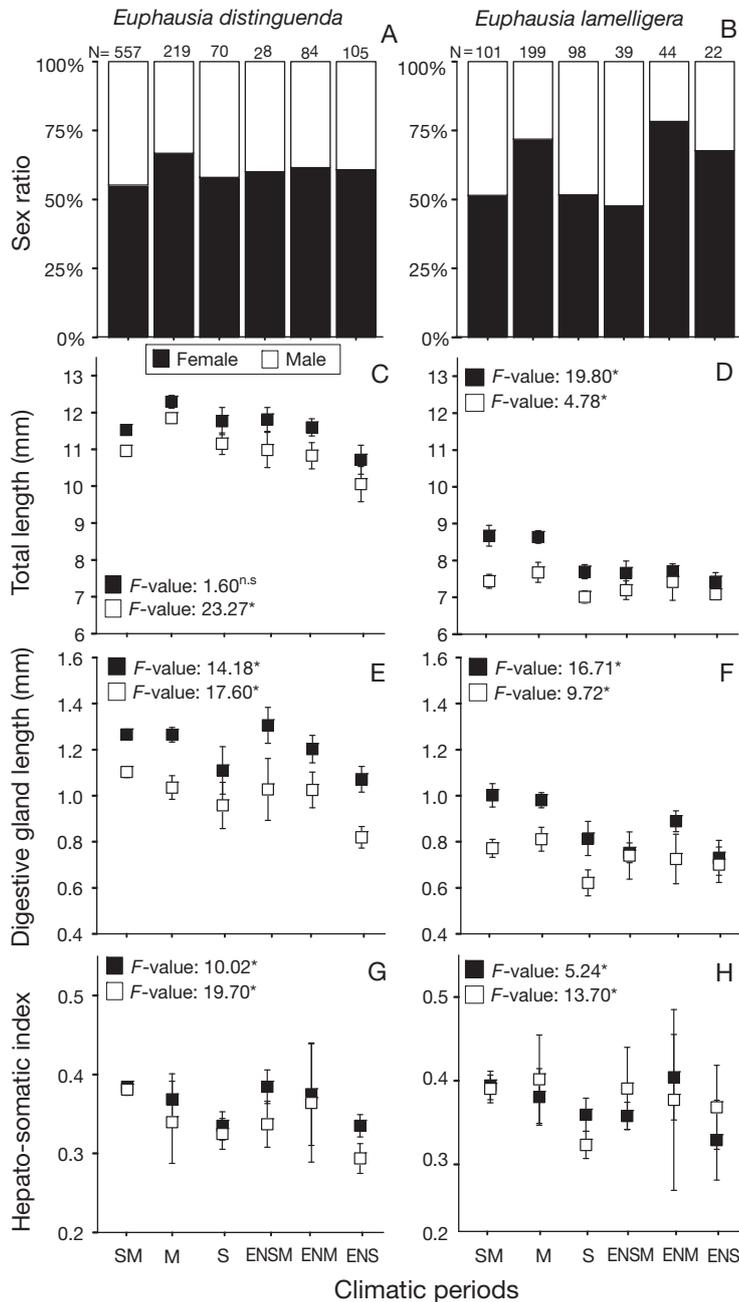


Fig. 7. *Euphausia distinguenda* and *E. lamelligera*. Seasonal variability of (A,B) sex ratio, (C,D) total length, (E,F) hepatopancreas length, and (G,H) hepato-somatic index (HSI) of *E. distinguenda* (A, C, E, G) and *E. lamelligera* (B, D, F, H) adults. Means ($\pm 95\%$ confidence intervals) per oceanographic periods as defined in Fig. 3. Results of ANOVA among periods are shown, indicating significance at $p < 0.001$ (*); ns: not significant. N = number of adult specimens measured during each sampling period

and therefore the mixed layer. In the Cabo Corrientes region, minimum phytoplankton biomass and phytoplankton production rates occur during a short downwelling period (July to November; López Sandoval et al. 2009a,b). We suggest that the strong thermohaline

seasonal variability in the upper water column of the neritic zone off Cabo Corrientes is mostly controlled by upwelling/ downwelling variability, atmosphere– ocean net heat flux, and freshwater input caused by rain/hurricane seasons (which increases precipitation and river discharges). Other meso-scale processes like eddies, fronts, and filaments may also induce significant changes in the upper layers (Lavín et al. 2006, Cepeda-Morales et al. 2009, Godínez et al. 2010, León-Chávez et al. 2010, Martínez-Flores et al. 2011).

On the interannual time scale, the most conspicuous environmental changes in the upper 100 m layer were caused by thermodynamic anomalies imposed by the El Niño of 1997–98. In June 1997, the first environmental signal of El Niño conditions was detected as a stronger seasonal variation induced by winds that increased upwelling activity between January and June 1998 (Fig. 2). The main environmental changes resulting from the 1997–98 El Niño event were the increase in surface temperature promoting pronounced changes in thermal stratification (homogeneously warm) and the deepening of the MLD (> 60 m). These changes in environmental patterns were caused by strong onshore advection of the Tropical Surface Water and Pacific Equatorial Superficial Water in the upper 90 m layer, an oceanographic response previously documented in the Cabo Corrientes region during this El Niño event (Filonov & Tereshchenko 2000). Surprisingly, during January to June 1998, upwelling conditions prevailed and the typically strong seasonal variability rapidly damped the 1997–98 El Niño event effect. The diatoms *Chaetoceros curvisetus*, *Leptocylindrus danicus*, and *Rhizosolenia stolterforthii* were positively associated with this comparatively high productivity cold-water period. Thus, intense upwelling events induced an increase in abundance of these 3 diatom species (and other species) and characterized this brief but intense 1997–98 El Niño event (Fig. 4D,E). Similarly, the plankton biomass (chl *a* concentration and zooplankton biomass) off the Baja California Peninsula ($32\text{--}24^\circ\text{N}$) was not considerably affected during the 1997–98 El Niño along the west coast of the Baja California peninsula (Lavaniegos et al. 2002). Contrary to our results, previous studies in the central

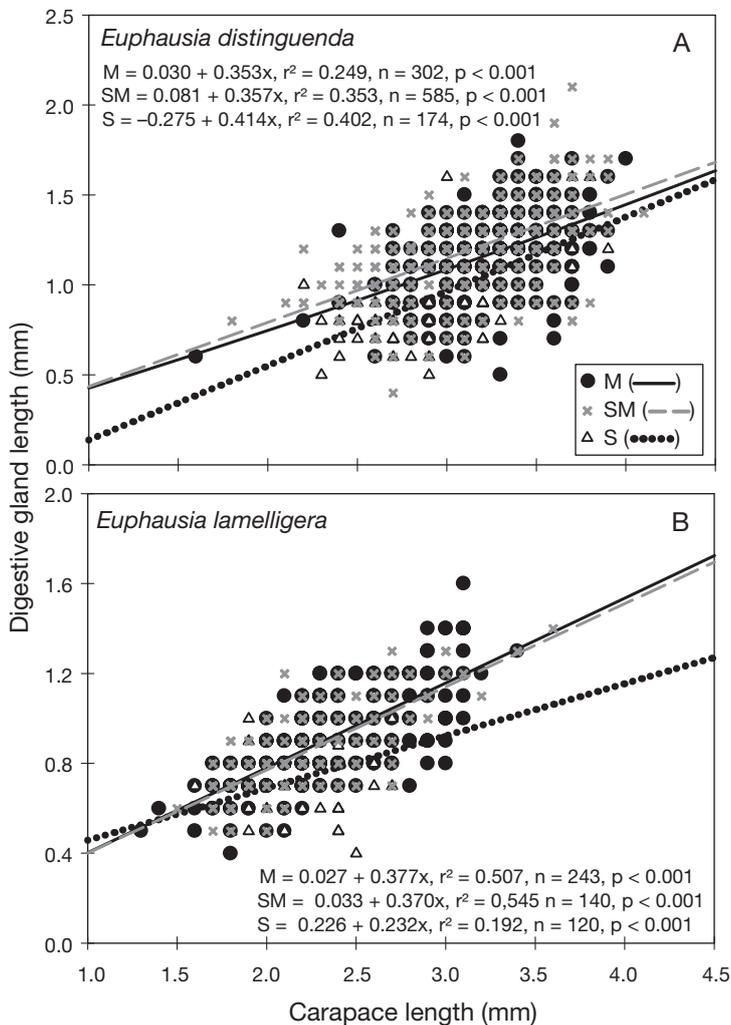


Fig. 8. *Euphausia distinguenda* and *E. lamelligera*. Linear regression model of the hepatopancreas length as a function of the carapace length from specimens collected during M, SM, and S periods (as defined in Fig. 3) for (A) *E. distinguenda* and (B) *E. lamelligera*

Mexican Pacific reported that the variability in the upper layer is mostly dominated by El Niño-induced anticyclonic circulation (Lavín et al. 2006, Godínez et al. 2010) and decreasing primary production (Chavez et al. 1999). Barber & Chavez (1983) suggested that inshore ecosystems are significantly less affected by El Niño events than offshore ecosystems, as may happen at the Cabo Corrientes region.

Seasonal/interannual variability of tropical euphausiids

We show evidence of strong seasonal variability of euphausiid abundance and relatively moderate 1996 to 1998 interannual changes in euphausiid community

structure and relatively low species diversity. Although the Mexican central Pacific is a tropical ecosystem with a relatively shallow oxygen minimum zone (Wyrtki 1967, Seibel 2011), the highest density of total euphausiid abundance occurred during the intense upwelling season (February to May). These seasonal changes were of the same order of magnitude as that reported in other upwelling regions of the Mexican sector of the California Current System. However, this tropical ecosystem has overall lower euphausiid biomass because most tropical species are considerably smaller (<13 mm TL) than subtropical and temperate species in the California Current (up to 25 mm TL; Brinton 1962, 1979, Lavaniegos 1994, 1995, Gómez-Gutiérrez 1995, 1996, Gómez-Gutiérrez et al. 1995, Brinton & Townsend 2003) and the Gulf of California (Brinton & Townsend 1980, Lavaniegos et al. 1989). Euphausiid abundance showed a strong seasonal cycle imposed by the 2 small-sized dominant tropical euphausiid species (*Euphausia distinguenda* TL <13 mm and *E. lamelligera* TL <9 mm; Fig. 5B–D). Multivariate analysis (RDA) confirmed that euphausiid abundance in this tropical coastal ecosystem was closely related to seasonal patterns of nano- and microphytoplankton abundance driven by upwelling–transition–downwelling (M, SM, and S) conditions. Samples collected between February and May were positively correlated with CUI on the sampling day, and those collected between July and November were negatively correlated with CUI (Fig. 6, Table 5). The RDA demonstrated that seasonal variability of euphausiid abundance and community structure was of

a larger magnitude than the interannual variability during the period studied. This seasonal pattern corresponded with the phytoplankton species composition and abundance. Franco-Gordo et al. (2004) included 12 sampling stations, in the same region, during a period of 3 yr (December 1995 to December 1998) of zooplankton biomass and fish larvae abundance and species composition. They reported that the highest zooplankton biomass and ichthyoplankton abundance occurred from January to May (period of intense upwelling events) every year. This pattern confirms that strong seasonal variability of wind-induced coastal upwelling events imposes a bottom-up control on merozooplankton and holozooplankton abundance and biomass in the southern Cabo Corrientes region (Fig. 2B).

The 8 euphausiid species detected during the 1996 to 1998 time series in the Mexican central Pacific have been previously reported in multiple oceanographic cruises carried out in the ETP region (Brinton 1962, 1979, Sánchez-Osuna & Hendrickx 1983, Gómez-Gutiérrez & Hernández-Trujillo 1994, Färber-Lorda et al. 2010). All of these previous offshore studies have reported that the neritic species *Euphausia lamelligera* is the numerically dominant euphausiid species of this tropical region. However, we detected that during 1996 to 1998, *E. distinguenda* was consistently the most abundant euphausiid species of the coastal region off the Cabo Corrientes region (100–130 m seafloor depth; Fig. 5B–D, Table 3).

In the Gulf of Tehuantepec, low *Euphausia distinguenda* larval abundance was recorded onshore from 25 oceanographic stations sampled in January 1989, suggesting that the coastal zone is not within its optimal reproductive area and/or distribution range for this species (Färber-Lorda et al. 1994). In the Cabo Corrientes region, the maximum larval abundance of *E. distinguenda* was detected during SM periods and during the 1997–98 El Niño event, suggesting onshore transport because this species is typically more abundant in offshore waters (Färber-Lorda et al. 2010). *E. distinguenda* had exceptional peaks of postlarval abundance during M periods (Fig. 5B–D). Thus, oceanographic conditions that prevailed along the Jalisco and Colima continental shelf were favorable for the *E. distinguenda* population, reported here for the first time as a numerically dominant species in a neritic region of the ETP. In fact, the RDA showed that *E. distinguenda* postlarvae increased their abundance and probably their reproduction (indicated by presence of calyptopis and mature adults) during active upwelling when phytoplankton abundance and chl *a* concentration reached their highest levels (López Sandoval et al. 2009a,b). The neritic *E. lamelligera* postlarvae were also abundant during the intense upwelling period having a strong positive correlation with CUI (Fig. 6B). Considering the relatively high proportion of larvae and adults of *E. distinguenda* and *E. lamelligera*, we propose that this coastal upwelling region is a relevant reproduction area for both krill species. This maximum abundance of euphausiids and reproduction periods showed a clear association with upwelling variability as reported in euphausiid species distributed at coastal zones of the Eastern Boundary Current upwelling ecosystems of California (Dorman et al. 2005), Humboldt (Riquelme-Bugueño et al. 2012), and Benguela (Barange & Stuart 1991, Pillar et al. 1992).

The euphausiid species richness considerably increased with the presence of larvae and juveniles of oceanic species such as *Euphausia diomedea*, *E. tenera*, *Stylocheiron affine*, *S. carinatum*, and *Nematoscelis gracilis* during the 1997–98 El Niño period (Fig. 5). This increase in species richness may indicate strong onshore advection of Tropical Surface Water and Subsurface Equatorial Water previously reported for this region (Filonov & Tereshchenko 2000). RDA showed that the temperature explained most of the euphausiid variability pattern of *N. gracilis*, supporting the idea of an onshore advection of warm water, indicated by the deepening of the thermocline, was likely the process that transported and even caused favorable conditions for proliferation of this tropical oceanic species assemblage along the continental shelf of Cabo Corrientes. A similar response to the 1997–98 El Niño was reported in the southern region of the California Current System where higher abundance of 3 unusual tropical species (*E. distinguenda*, *E. tenera*, and mainly *E. eximia*) along the west coast of the Baja California peninsula (Ambriz-Arreola 2007) and northward advection of the subtropical neritic species *Nyctiphanes simplex* in waters from California to Canada (Brodeur 1986, Mackas & Galbraith 2002, Marinovic et al. 2002, Peterson et al. 2002, Tanasichuk & Cooper 2002, Feinberg & Peterson 2003, Keister et al. 2005). These species were indicators of strong onshore and poleward flow of warm water forced by different El Niño events.

Other evidence of the upwelling effects on *Euphausia distinguenda* and *E. lamelligera*

HL and the HSI were useful indicators of seasonal krill trophic condition, showing significantly higher HSI values during the M and SM periods (when phytoplankton peaked) than during S periods (when phytoplankton had their lowest values; Fig. 7). The hepatopancreas of crustaceans serves the dual role of secreting enzymes and absorbing digested food. Specifically, the hepatopancreas assists in the depolymerization of (1→3)- β -D-glucans in the euphausiid diet (McConville et al. 1986), being a sensitive indicator of recent and long-term trophic conditions of *Euphausia superba* (Endo & Kadoya 1991, Shin 2000, Virtue et al. 2010, O'Brien et al. 2011) and *E. crystallorophias* (Nicol et al. 2004) in Antarctic ecosystems. These studies demonstrated that HL of these polar krill species was strongly associated with the seasonal and inter-annual variability in food

abundance or dietary shifts. Our results suggest that tropical euphausiids are also sensitive to seasonal changes in food availability.

The sex ratio of *Euphausia distinguenda* and *E. lamelligera* was typically close to 50:50 throughout the 1996 to 1998 time series. However, the decrease in the proportion of males during column water M periods suggests that both species are exposed to different predation rates or that males and females have distinct vertical migration patterns when the ratio departs from 50:50 (Fig. 7A,B). In Antarctic krill, it was demonstrated that males grow faster but die younger than females (Kawaguchi et al. 2007), and this pattern might also hold for tropical species under mixed column water conditions. Tirling (2003) mentioned that selective mortality, either through physiological differences between sexes or sex-specific predation, is the major factor responsible for the substantial sex ratio variability in *Meganyctiphanes norvegica*. Hill et al. (1996) also found evidence that males of *E. superba* in the northwest of South Georgia evade nets and predators such as macaroni penguins *Eudyptes chrysulophus* more efficiently than females. These studies provide insight into explaining possible mechanisms of departure from standard sex ratios in the Cabo Corrientes region. A closer examination of top-down control processes alongside studies of the physiological capacity of tropical krill are also required to gain a fuller understanding of the operation of this tropical ecosystem.

In conclusion, we provide evidence that temporal variability in upwelling/downwelling is a key coastal mechanism in the seasonal regulation of euphausiid species composition, abundance, and likely the plankton productivity of this tropical ecosystem. We also demonstrate that seasonal upwelling–downwelling variability in Cabo Corrientes forced a larger bottom-up influence than the 1997–98 El Niño conditions. Our study will provide baseline information for future work focused on the comparisons among zooplankton time series from different ocean regions that, according to Mackas & Beaugrand (2010), will represent a critical step to predict the likely amplitude and steepness of future climate changes in marine ecosystems.

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