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Research Article

Copepod community structure and functional feeding groups off the Central Mexican Pacific (spring of 2015)

Susana Cabrera-Núñez[1,2], Roxana De Silva-Dávila[3] & Sergio Hernández-Trujillo[3]
[1]Programa de Maestría en Manejo de Recursos Marinos, Centro Interdisciplinario de Ciencias Marinas
Departamento de Plancton y Ecología Marina, Instituto Politécnico Nacional
La Paz, B.C.S., México
[2]Programa de Postgrado en Oceanografía, Departamento de Oceanografía
Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile
[3]Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas
Instituto Politécnico Nacional, La Paz, B.C.S., México
Corresponding author: Sergio Hernández-Trujillo (strujil@ipn.mx)

ABSTRACT. Copepods respond rapidly to ecosystem variability at different spatial-temporal scales as part of the pelagic ecosystem and marine trophic webs. This work addresses the lack of knowledge of the copepods community's response to environmental changes in the convergence of the water masses and marine currents of the Central Mexican Pacific (CMP). Zooplankton samples (April 2015) from vertical hauls (100-0 m) and water column environmental variables from CTD casts were obtained. Warm environmental conditions predominated in the CMP due to El Niño 2014-2015. Copepod abundance community is distributed homogeneously without statistical differences in the community structure, collection time, ecological indexes, or functional feeding group. The dominant species were *Subeucalanus subcrassus*, *Centropages furcatus*, and *Subeucalanus mucronatus*. The exclusion of the dominant and abundant species from our statistical analyses allowed us to determine latitudinal differences in the underlying community structure. Statistical analysis (similarity percentage analysis and canonical correspondence analysis) identified three species-sampling stations groups (north, south, pacific) with significant differences in the community composition and functional feeding groups related to contrasting environmental conditions, particularly in the north *vs*. the south of the CMP related to dissolved oxygen, salinity, and chlorophyll-*a* concentrations gradients, and to the influence of local and mesoscale oceanographic and biological processes registered in the water column despite the homogeneous tropical conditions. This first approach to the copepod community structure of the CMP also gave us information about the water column environment during a period affected by warm conditions due to El Niño 2014-2015, identifying areas of high productivity with possible effects at higher trophic levels.

Keywords: Copepoda; El Niño 2014-2015; latitudinal changes; functional feeding groups; vertical profiles

INTRODUCTION

Copepods represent between 60-90% of zooplankton and have a significant role in marine biogeochemical cycles by linking primary production with secondary consumers (Fernández-Álamo et al. 2000, Hernández-Trujillo & Esqueda-Escárcega 2002, López-Ibarra et al. 2014). Their distribution and abundance are influenced by hydrodynamic processes at different spatial and temporal scales and by their rapid response to this variability through changes in the structure of their communities (Kozak et al. 2014), which allows them to be considered environmental indicators since the analysis of copepod communities help to determine water masses (Gael et al. 2007).

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These crustaceans have different feeding habits (herbivory, omnivory, carnivory, parasitism, and detritivory) and occupy one or more trophic levels throughout their life cycle. Their high abundance, short life cycle, size, and distribution in the water column make them an important item in the diet of other zooplankters, including species of commercial importance in their larval stages, such as fishes and cephalopods (Uchikawa et al. 2009, Camarillo-Coop et al. 2013). Still, also this relationship is both ways, so they compete and prey on these components (Palomares-García & Vera-Alejandre 1995, Palomares-García et al. 2018). The study of the feeding groups of copepods becomes a priority as they can show functional differences in the ecosystems (Benedetti et al. 2016, Venelleo et al. 2021).

In the Mexican Pacific, studies on the ecology of marine pelagic copepods, analyzing the community composition and structure, feeding habits, and their relation with the environment are still scarce (Suárez-Morales et al. 2000, Siordia-Cermeño et al. 2003, Kozak et al. 2013, 2014, 2018, 2020, López-Ibarra et al. 2014, 2018, Rojas-Herrera et al. 2016) with a limited sampling effort in terms of spatial and temporal coverage. In this region, 197 species of pelagic copepods have been recorded (Hernández-Trujillo & Esqueda-Escárcega 2002); in the Central Mexican Pacific (CMP) off the coast of Jalisco to Guerrero, this number is imprecise, although Kozak et al. (2013) identified 82 species in Jalisco and Colima. *Subeucalanus subcrassus* and *Centropages furcatus* stand out for their dominance among the identified species.

The convergence of cold and warm water masses and marine currents in the CMP generates environmental conditions whose effects on the copepod community have yet to be studied. In this research, we describe the community structure of copepods in the neritic and oceanic zones, also their trophic functional groups between Cabo Corrientes, Jalisco, and the Bay of Acapulco, Guerrero, Mexico, by latitudinally comparing their spatial distribution with hydrographic variables.

MATERIALS AND METHODS

Study area

The CMP includes the coasts of the states of Jalisco to Chiapas, having a narrow continental shelf (10 to 15 km) (Fig. 1). In the coastal region, the sea surface temperature (SST) oscillates between 26-28°C, with little variability. The thermocline depth is determined by variations in the distribution of cold water in a west-east direction by the wind, registering a depth of 40 m in the northern area. In comparison, in the south, it is shallower (20 m) (Wilkinson et al. 2009, CONANP 2018).

In the spring (March-June), the SST is between 24-28°C with a shallow thermocline in the north that deepens to the south. The net evaporation of the water surface in the CMP explains the high salinity (S, 34.6-35.1) registered. The surface flow of the main water masses: Gulf of California Water (GCW) (temperature, T > 12°C, S > 35.1) and California Current Water (CCW, 10°C < T < 21°C, S < 34.6) is southward, while the Tropical Surface Water (TSW), (T > 25.1°C, S < 34.6) flows in a northern direction. The Transitional Water (TW), originated by the mixture of GCW and TSW, is present along the entire coast (Wilkinson et al. 2009, Pantoja et al. 2012, Gómez-Valdivia et al. 2015, Portela et al. 2016, CONANP 2018). The convergence of water masses in this zone converts the CMP into a complex region where mesoscale meanders, filaments, thermal fronts, and intense eddy activity dominate (Lavín et al. 2006, Pantoja et al. 2012, Portela et al. 2016). The oxygen minimum zone (OMZ) is detectable from 50 m depth. It is susceptible to the influence of mesoscale processes, but it's spatial-temporal variability and relationship with dynamic aspects are unknown (Cepeda-Morales et al. 2009, CONANP 2018).

The high oceanographic variability in the CMP includes three main time-space scales: a) the seasonal flux of the poleward coastal current (Mexican Coastal Current, MCC) during spring to autumn, and the equator-ward current (California Current, highly modified and without a clear southern limit) during the rest of the year; b) the presence of eddies, filaments, and upwelling events over days, weeks or months; c) the El Niño Southern Oscillation that causes interannual variation, and high precipitation rates occurring in the Cabo Corrientes region during summer (Ambriz-Arreola et al. 2012, Gómez-Valdivia et al. 2015). A conspicuous seasonal hydrographic cycle in the Cabo Corrientes region prevails, influencing phytoplankton biomass and plankton communities. Upwelling events occur from February to May and favor local increases of the primary production; these were 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).

Sampling and processing of samples

Zooplankton samples were obtained from the oceanographic campaign "Marea Roja-VII," carried out in

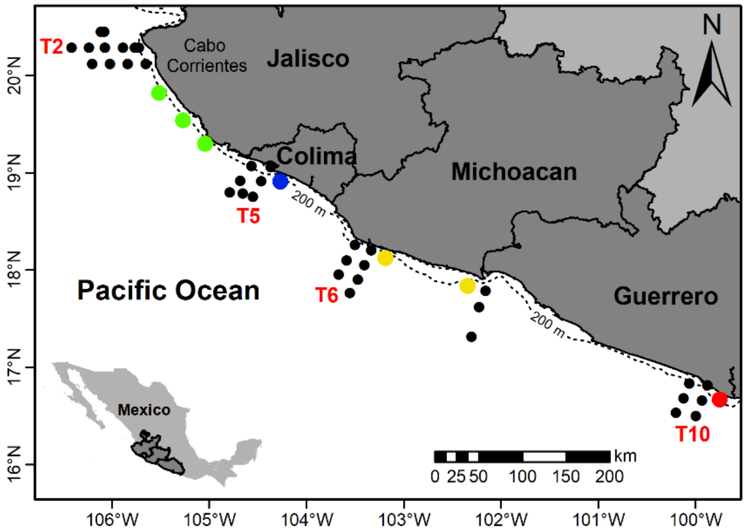

Figure 1. Study area and sampling stations off the Central Mexican Pacific (April 2015). Zone: Jalisco, Colima, Michoacan and Guerrero. Sampling stations used (CTD haul) to construct the vertical profiles presented in Figure 2: green: Jalisco, blue: Colima, yellow: Michoacan, red: Guerrero. Dotted line: isobath of 200 m depth.

early spring from April 13 to 25, 2015, on board the B/O El Puma, with 42 neritic and oceanic sampling stations, distributed in 10 transects perpendicular to the coast, between Cabo Corrientes, Jalisco, and Acapulco Bay, Guerrero, Mexico (20.7-16.3°N and 105.3-98.5°W) (Fig. 1).

In each sampling station, a Sea-Bird 19 plus (0-120 m) CTD cast was made, recording T (°C), S, dissolved oxygen (DO, mL L^{-1}), and fluorescence. For DO, the isoline of 0.7 mg L^{-1} (equivalent to 0.5 mL L^{-1}) was identified as the upper limit of the OMZ (Hendrickx & Serrano 2010, Maske-Rubach et al. 2017); for fluorescence, it was obtained from using the ECO-AFL/FL (chlorophyll, Chl-*a*, mg m^{-3}) calibration coefficients for voltage sensors according to Sea-Bird Scientific (2017) software manual. Water column profiles for all sampling stations were constructed with the CTD data; since the greatest changes in the water column were of T and Chl-*a*, only the vertical distribution of these two variables in four selected transects (T2, T5, T6, and T10) is presented here.

To detect mesoscale processes that could influence the copepod community, satellite images of SST and Chl-*a* concentration were analyzed using GOES-11 and Aqua Modis sensors (L3 processing level at 4 km resolution) (NASA 2023a, 2023b). The profiles were processed using the Ocean Data View 4 program and the satellite images with Surfer V13 from Golden Software.

Zooplankton samples were obtained during the day and night according to the time of arrival at the sampling station by vertical hauls (100-0 m) using a cylindrical-conical net of 1.5 m length, with a mesh size of 333 µm and mouth opening with a diameter of 0.60 m. A flowmeter (General Oceanics®) was attached to the mouth of the net to estimate the amount of water filtered. The samples were preserved with a 4% formalin solution buffered with sodium borate. The copepods were separated, identified, and counted completely from samples with <60 mL of biovolume. Samples with a larger biovolume were diluted to a known volume of the same fixative solution and stirred gently. A Stempel pipette was then used to obtain 12.5 mL subsamples (Hernández-Trujillo et al. 2010).

The copepods were identified using a Stemi DV4 stereoscopic microscope (Carl Zeiss) following the morphological criteria of Palomares-García et al. (1998), Razouls et al. (2005-2022), and classified according to Walter & Boxshall (2022). Its abundance was standardized to individuals in a thousand cubic meters of filtered water (ind 1000 m^{-3}) (Kramer et al. 1972). Day-night abundance differences were statistically tested using a Kruskal-Wallis test (Ostertagová et al. 2014).

Community structure

Models for specific richness (SR), Shannon-Wiener diversity (H'), and Simpson dominance (λ) were estimated (Daly et al. 2018), while the species classification in functional groups was performed according to their feeding type (herbivores, carnivores, omnivores, and parasites) using the criteria of Longhurst (1985), López-Ibarra et al. (2014, 2018), Benedetti et al. (2016), Kozak et al. (2020) and Walter & Boxshall (2022).

The initial analysis of all copepod species abundance throughout the study area showed a homogeneous distribution probably caused by the dominant species abundance. Therefore, the 13 dominant and abundant species (*Subeucalanus subcrassus*, *S. mucronatus*, *Centropages furcatus*, *Oithona setigera*, *Acrocalanus gibber*, *Canthocalanus pauper*, *Oncaea venusta*, *Clausocalanus jobei*, *Temora discaudata*, *Pleuromamma gracilis*, *Corycaeus speciosus*, *Paraeuchaeta incisa*, and *Scolecithrix danae*) were extracted from the database. The remaining species were then reanalyzed to detect their abundance and distribution differences along the CMP.

A two-way cluster analysis was performed to identify patterns of regionalization of abundance and possible associations between species using the PC-ORD 6.0 software (MjM Software Design) applying the Bray-Curtis ordination index with a flexible beta of 0.25 as a linkage method (Legendre & Legendre 2012, Peck 2010). Also, a similarity percentage analysis (SIMPER) was used to calculate the contribution of the abundance of each taxon to the similarity within and between the groups of copepods (obtained from clustering analysis) and of the abundance of functional feeding groups with the PRIMER-6$^{©}$ software.

A canonical correspondence analysis (CCA) was also calculated to explore the copepod species abundance (without dominant and abundant species) and the environmental relationship. The species abundance-environmental conditions data were log (x+1) transformed to decrease variance and linearize variables (McCune & Mefford 2011). The environmental variables T, S, DO, and Chl-*a* were averaged for the water column (0-100 m depth) and analyzed to identify the most influential environmental gradients on copepod abundance applying a Monte Carlo test to 999 permutations calculated with the statistical program CANOCO 4.5. The mean values of the environmental variables used here represent more likely the conditions of the water column (0-100 m) sampled in our study than a single surface or 10 m depth values used in other copepod and zooplankton canonical analyses in the area (De Silva-Dávila et al. 2015, Beltrán-Castro et al. 2020, Martínez-Soler et al. 2021).

RESULTS

Oceanographic structure

The water column in the neritic portion of the CMP showed a stratified column with a mean SST of 26°C but warmer SST with lower salinity in the southern region; also, the thermocline, halocline, and oxycline depths were distributed in the first 30 m depth (Figs. 2a,-c). The Chl-*a* concentration showed two subsurface maximums between 20-40 m and at 90 m depth (Fig. 2d). The upper limit of the OMZ varied latitudinally from 30 m in the north to 80 m in the southern region (Fig. 2c), with the presence of TW between 20-45 m depth below the TSW (>25.1°C, 0-20 m). At the end of the sampling, the SST was warmer (27-30°C) towards the south of the study area (Figs. 3a,c), while the surface Chl-*a* concentration registered the maximums in Jalisco. Conversely, the south (Guerrero) showed onshore-offshore Chl-*a* filaments in both cruises (Figs. 3b,d).

In Jalisco, the T2 transect was influenced by a mesoscale cyclonic gyre with the near-shore edge with relatively cooler water and high Chl-*a* and the opposite oceanic edge with warmer water and lower Chl-*a* concentrations (Figs. 3a-b) associated with a Subtropical Subsurface Water (StSsW) elevation located between 40-120 m, occupying most of the water column and the maximum subsurface Chl-*a* (5 mg m^{-3}) between 20-40 m depth from 40 km in the neritic-oceanic direction (Figs. 4a-b). In Colima (T5), a narrow coastal zone with high Chl-*a* values was observed (Fig. 3), while in the oceanic portion 30 km offshore, an elevation of TW was detected, with a thermal difference of 4°C between the neritic and oceanic zones and the subsurface maximum of Chl-*a* (6.89 mg m^{-3}) (Figs. 4c-d). In Michoacan (T6), the superficial productive zone expanded compared to that of Colima, associated with the SST decrease (Fig. 3). The maximum Chl-*a* (9.41 mg m^{-3}) was located from the surface to 40 m depth within the distribution of the TW (Figs. 4a-b). A wide productive surface coastal zone was observed in the south (T10). Also, an increase in the SST values (30°C) and Chl-*a* (19 mg m^{-3}) in a neritic-oceanic trend, being shallower in the coastal portion and deep (0-40 m) at 80 km (Fig. 4g).

Despite the environmental gradients between the regions, mesoscale processes, and the differences between the neritic and oceanic zones, we did not find significant statistical differences for any environmental surface variable along the CMP (T: $H_{(3, 42)} = 1.81$, $P = 0.61$; S: $H_{(3, 42)} = 7.4$, $P = 0.06$; DO: $H_{(3, 42)} = 2.75$, $P = 0.43$; Chl-*a*: $H_{(3, 39)} = 5.79$, $P = 0.12$).

Copepod community structure

The mean abundance of copepods along the CMP was 13,411 ind 1000 m^{-3}, and the mean abundance by zones showed a maximum in Jalisco (16,622 ind 1000 m^{-3}) and a minimum in Michoacan (9811 ind 1000 m^{-3}). The

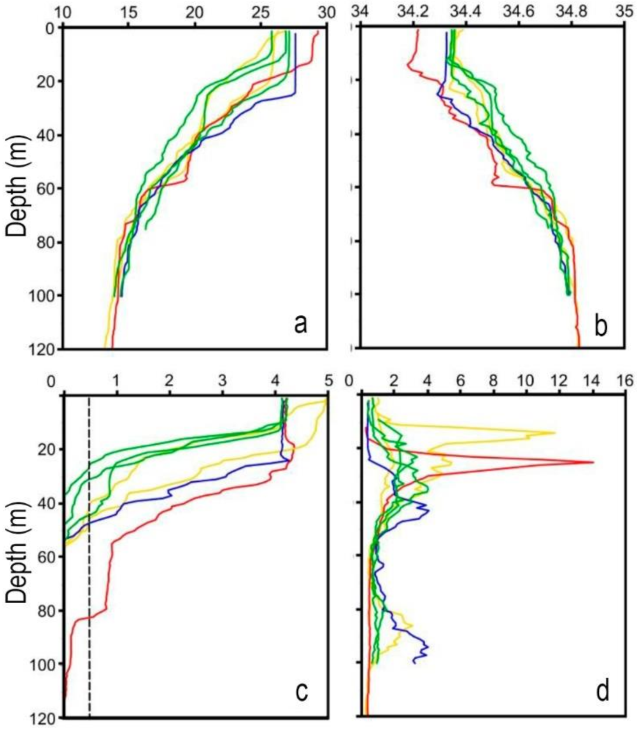

Figure 2. Vertical profiles of a) temperature (°C), b) salinity, c) dissolved oxygen (mL L^{-1}), and d) chlorophyll-*a* (mg m^{-3}) in the coastal stations of Central Mexican Pacific. The dashed line indicates concentrations of 0.5 mL L^{-1}. Green lines: Jalisco, blue line: Colima, yellow lines: Michoacan, red line: Guerrero. Colored lines are the sampling stations (CTD hauls) used to construct the vertical profiles in the different zones (See figure).

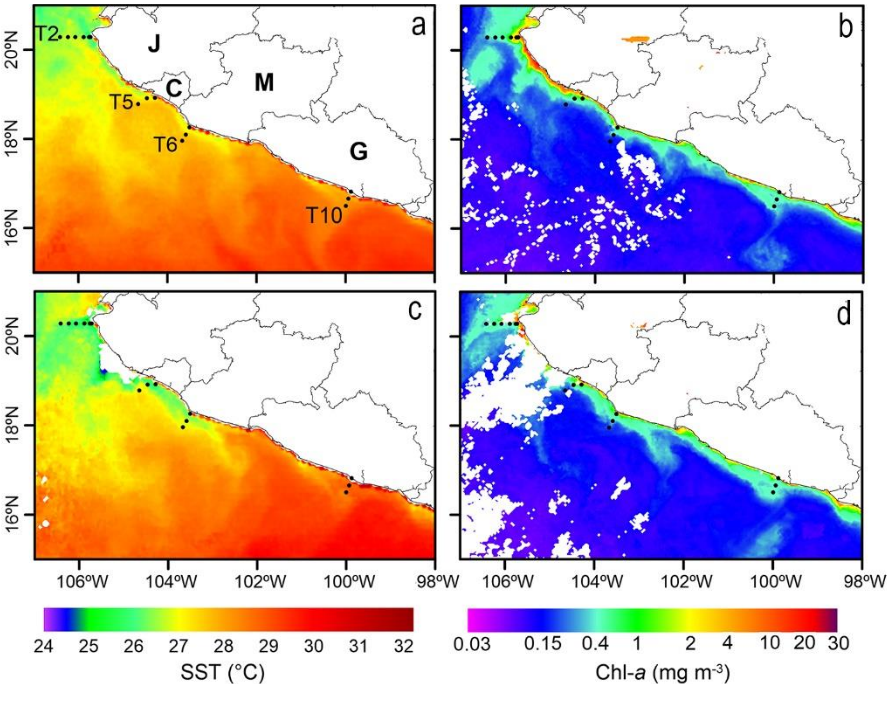

Figure 3. Weekly satellite images of: a,c) sea surface temperature, b,d) chlorophyll-*a* concentration, of onset (a-b, April 16, 2015) and end (c-d, April 23, 2015) of the oceanographic campaign in the Central Mexican Pacific, Mexico. Black circles: sampling stations of selected transects. White areas indicate clouds. Zones: J: Jalisco, C: Colima, M: Michoacan, G: Guerrero.

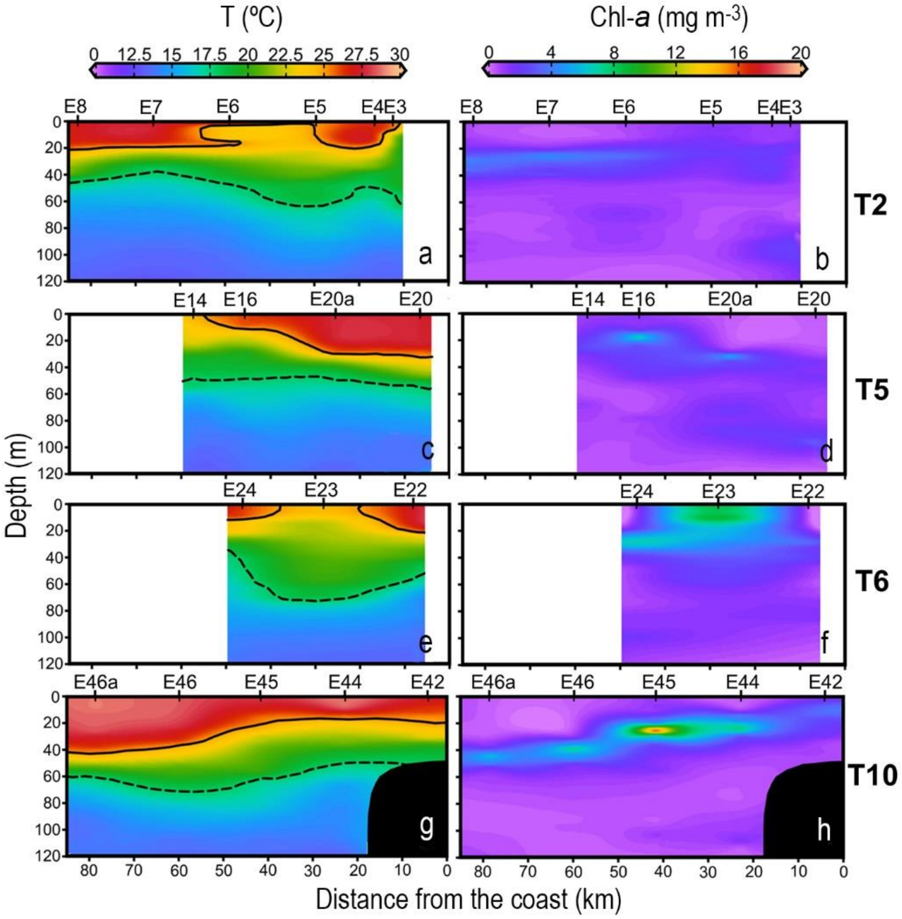

Figure 4. Cross-shore section of a) temperature (T, °C), and b) chlorophyll-*a* concentration (Chl-*a*, mg m^{-3}) in the first 120 m depth in the four transects selected (T2, T5, T6, and T10, see Figure 1). Black continuous line: 25.1°C isotherm (lower limit of the Tropical Surface Water); dashed line: 18°C isotherm (upper limit of the Subsurface Subtropical Water).

CMP recorded a homogeneous species richness with an average of 25 species, the maximum in Colima (29 species) and the minimum in Michoacan (~20 species) (Fig. 5a). Mean diversity was 3.38 bits ind^{-1}, with similar values from Jalisco to Michoacan (3.14 to 3.34 bits ind^{-1}), but the highest diversity in Guerrero (3.83 bits ind^{-1}) (Fig. 5a). Mean values of Simpson dominance (0.18 to 0.19) were recorded in Jalisco, Colima, and Michoacan, and the minimum in front of Guerrero (0.11). These values were inverse to those of diversity (Fig. 5a).

Three orders: Calanoida, Cyclopoida, and Harpacticoida; 24 families, 35 genera, and 60 species of copepods were identified (Table 1). Five species made up 62% of the total abundance of copepods in most of CMP: *Subeucalanus subcrassus* (28%), *Centropages furcatus* (16%), *Subeucalanus mucronatus* (7%), *Oithona setigera* (6%), and *Acrocalanus gibber* (5%), were the dominant and the most abundant. The remaining 55 species contributed 38%, with an increasing trend southward. Most species were tropical-subtropical (93%). The species *S. subcrassus* and *C. furcatus* decreased in abundance latitudinally from north to south (Fig. 5b).

Omnivorous (65%) and carnivorous (24%) copepods were the most abundant in the CMP, followed by herbivores (10%) and parasites (1%). Omnivores were more abundant in Jalisco and Michoacan, decreasing by 10-15% in Colima and Guerrero. Meanwhile, the carnivores were more abundant. In Jalisco and Colima, herbivores accounted for 12% of the community, decreasing in Michoacan and Guerrero. Parasitic species were lower than 1% in the study areas (Fig. 5c).

The abundance of the dominant species did not allow us to identify significant differences in the copepod's structure community along the CMP by zone: $H_{(3, N = 42)} = 3.60$, $P = 0.31$ or time (day-night): $H_{(1, N = 42)} = 1.36$, $P = 0.24$. Also, the homogeneity of the copepod community was observed through the ecological indexes that showed no significant differences in

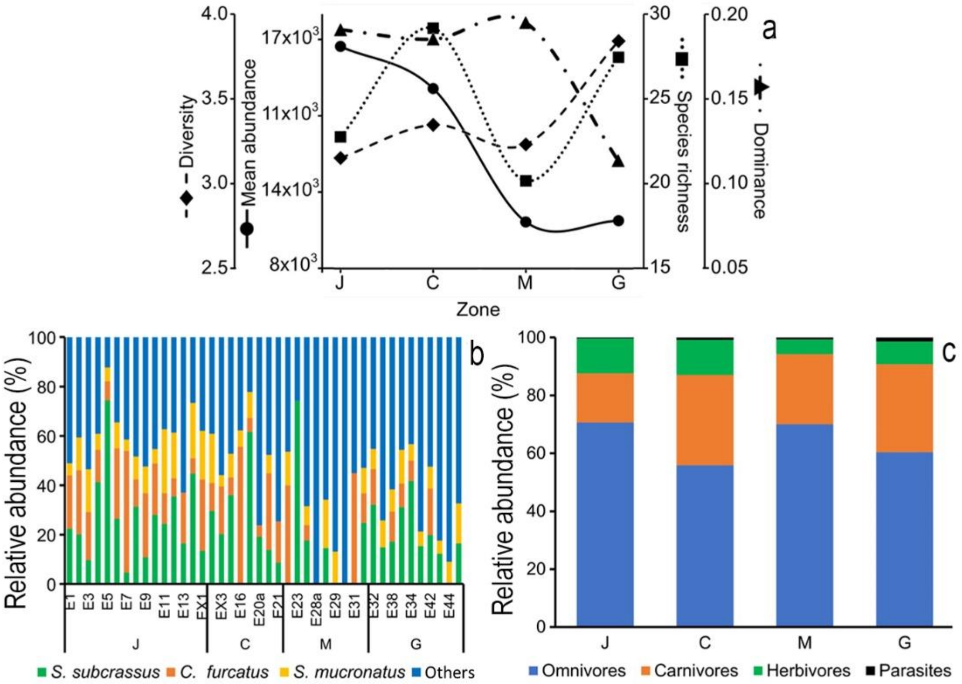

Figure 5. a) Copepods community attributes by zone in the Central Mexican Pacific (April 2015) (diversity: bits ind^{-1}; mean abundance: ind 1000 m^{-3}), b) relative abundance of dominant species and the rest of the species grouped, c) relative abundance of the feeding functional groups by zone: J: Jalisco, C: Colima, M: Michoacan, G: Guerrero.

species richness ($F_{(3, 34)} = 0.89$, $P = 0.46$), diversity ($F_{(3, 34)} = 0.55$, $P = 0.65$) or dominance ($F_{(3, 34)} = 0.32$, $P = 0.81$) and it was the same result for the functional feeding groups (carnivores: $H_{(3, 40)} = 2.23$, $P = 0.53$; herbivores $H_{(3, 40)} = 2.99$, $P = 0.40$; omnivores $H_{(3, 40)} = 2.64$, $P = 0.45$, and parasites $H_{(3, 40)} = 2.10$, $P = 0.55$).

After removing the dominant and abundant species already mentioned, the cluster analyses of the community identified three different copepod groups by abundance and frequency: 1) north, including the abundant species distributed in front of Jalisco and Colima, 2) south, included species with low abundance and frequency in front of Michoacan and Guerrero, and 3) pacific, with species distributed along the entire CMP area with different abundances (Fig. 6).

The SIMPER analysis showed a dissimilarity greater than 67% among the groups: the north and the south groups were the most dissimilar (72.2%) (Table 2). In the pacific group, seven species contributed to 81% of the variation, with *Onychocorycaeus catus* and *Labidocera acuta* standing out. Eight species accounted for 83% of the variation in the north group, where *S. subtenuis* doubled its percentage, and *Pleuromamma abdominalis* increased almost ten times compared to the pacific group. *Cosmocalanus darwinii*, *Sapphirina scarlata*, and *Copilia quadrata* were common in the north and south groups. The species only recorded in the north group were *Paracalanus parvus* and *Rhincalanus nasutus* (Table 2). In the south group, 10 species contributed to 84% of the variation, with *Copilia mirabilis* contributing a maximum of 16%, which was lower than in the other groups where the maximum percentage for a single species was greater than 24%. In this group, *C. mirabilis*, *Undinula vulgaris*, *Euchaeta marina*, *E. longicornis*, and *O. catus* were common in the north and pacific groups. The first three increased their contribution percentage by over 50% compared to the other two groups. The species recorded only in the southern group were *Aetideus bradyi*, *Sapphirina metallina*, *Scolecitrichopsis ctenopus*, and *Candacia catula* (Table 2).

The functional feeding groups analyzed based on the SIMPER showed that in the pacific group dominated carnivore copepods (55%), such as *O. catus* and *L. acuta*. The north group was represented by omnivorous *S. subtenuis* and *P. abdominalis* (45%), and the south group by carnivores (56%) as *C. catula*, with an increase in herbivorous species (19%) represented by *U. vulgaris* and parasites (9%) such as *S. metallina* and *Microsetella rosea* in this area, compared to the north and pacific groups.

Table 1. General information of all the species identified in the Central Mexican Pacific. A: acronym, GF: functional feeding group; C: carnivores, H: herbivores, O: omnivores, P: parasites. The numbers indicate the groups resulting from the similarity percentage analysis analysis (Table 2): 1: north, 2: pacific, 3: south.

Species	A	GF	Species	A	GF
Acrocalanus gibber	Agib	H	*Candacia truncata*	Ctru	C
Clausocalanus jobei	Cjob	H	*Pachos punctatum*	Ppun	C
Cosmocalanus darwinii	Codar (1)	H	*Candacia simplex*	Csim	C
Undinula vulgaris	Uvul (3)	H	*Pleuromamma gracilis*	Pgra	C
Acartia (Acartiura) clausi	Acla	H	*Pleuromamma abdominalis*	Pabd (1)	C
Paracalanus parvus	Ppar (1)	H	*Pleuromamma* sp.	Ple	C
Nannocalanus minor	Nmin (2)	H	*Subeucalanus subcrassus*	Ssubc	O
Nannocalanus spp.	Nan.	H	*Subeucalanus mucronatus*	Smuc	O
Calocalanus pavo	Cpav (3)	H	*Subeucalanus subtenuis*	Ssubt (1)	O
Euchirella rostrata	Eros	H	*Centropages furcatus*	Cfur	O
Euchirella sp.	Euc sp.	H	*Temora discaudata*	Tdis	O
Eucalanus californicus	Ecal	H	*Scolecithrix danae*	Sdan	O
Euchirella amoena	Eamo	H	*Subeucalanus* sp.	Sub	O
Oithona setigera	Oset	C	*Aetideus bradyi*	Abra (3)	O
Canthocalanus pauper	Cpau	C	*Scolecitrichopsis ctenopus*	Scte (3)	O
Oncaea venusta	Oven	C	*Rhincalanus nasutus*	Rnas (1)	O
Euchaeta sp.	Euc	C	*Scolecithrix* sp.	Sco	O
Corycaeus speciosus	Cspe	C	*Subeucalanus crassus*	Scra	O
Paraeuchaeta incisa	Pind	C	*Gaetanus robustus*	Grob	O
Euchaeta longicornis	Elon (2)	C	*Gaetanus* sp.	Gae sp.	O
Corycaeus sp.	Cor	C	*Pseudodiaptomus wrighti*	Pwri	O
Corycaeus crassiusculus	Ccra (2)	C	*Gaetanus brevispinus*	Gbre	O
Onychocorycaeus catus	Ocat (2)	C	*Scolecithrix bradyi*	Sbra	O
Copilia mirabilis	Cmir (3)	C	*Centropages elongatus*	Celo	O
Euchaeta marina	Emar (3)	C	*Sapphirina scarlata*	Ssca (1)	P
Oithona sp.	Oit	C	*Sapphirina metallina*	Smet (3)	P
Labidocera acuta	Lacu (2)	C	*Sapphirina opalina*	Sopa	P
Labidocera sp.	Lab	C	*Sapphirina* sp.	Sap sp.	P
Oncaea sp.	Onc	C	*Sapphirina angusta*	Sang	P
Oithona tenuis	Oten	C	*Saphirella tropica*	Stro	P
Candacia catula	Cncat (3)	C	*Sapphirina darwini*	Sdar	P
Copilia quadrata	Cqua (1)	C	*Sapphirina nigromaculata*	Snig	P
Oithona plumifera	Oplu	C	*Clytemnestra scutellata*	Csco	P
Euchaeta media	Emed	C	*Microsetella rosea*	Mros	P
Pontellina plumata	Pplu (2)	C	*Sapphirina gemma*	Sgem	P
Canthocalanus sp.	Can	C	*Sapphirina intestinata*	Sint	P
Copilia sp.	Cop sp.	C	*Sapphirina stellata*	Sste	P

Copepod abundance and environment

The two first axes of the CCA explained 73.4% of the accumulated variance in the species-environment relationship (Table 3), with relatively low but significant correlations on axis 1 (F = 2.277, $P < 0.02$) and in the other axes (F = 1.392, $P < 0.02$). On axis 1, the DO was the environmental variable with the highest correlation (0.4803), followed by S (-0.3652). On axis 2, Chl-*a* had the highest correlation (0.6848).

The CCA's biplots showed the separation of sampling stations of the north located in a more saline and cooler environment than the sampling stations of the south distributed mainly in a warmer, less saline, and more productive environment with high concentrations of DO. The sampling station of the pacific group was present along the entire environmental gradients (Fig. 7a). Omnivorous (*S. subtenuis*, *R. nasutus*, and *G. robustus*), herbivores (*C. darwinii*,

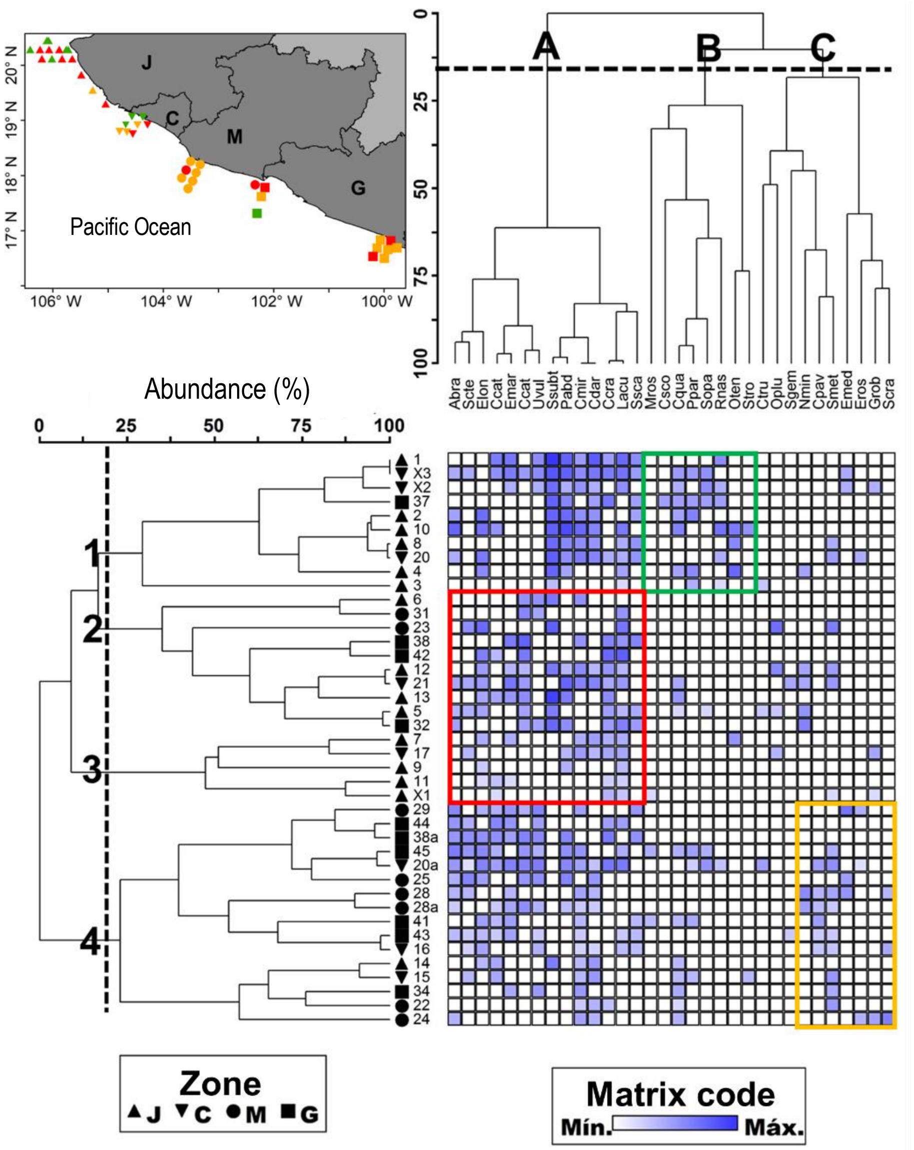

Figure 6. Two-way cluster analysis of the copepod community in the Central Mexican Pacific. Zones: J: Jalisco, C: Colima, M: Michoacan, G: Guerrero. A, B, C: species groups. Acronyms of the species are shown in Table 1. 1, 2, 3, 4: stations groups. Species-station clustering: 🟩: north group, 🟥: pacific group, 🟨: south group.

and *P. parvus*), and carnivores (*P. abdominalis*, *C. crassiusculus*, and *C. mirabilis*) were associated with the north sampling stations at S values of 34.53-34.66, low DO values (1.14-2.90 mL L^{-1}), and Chl-*a* between 0.97-1.46 mg m^{-3} (Fig. 7b). In contrast, more species of the parasitic feeding group (*M. rosea*, *S. metallina*, and *S. gemma*) and herbivores (*U. vulgaris*, *C. pavo*, and *N. minor*) associated with high DO values (1.33-3.24 mL L^{-1}), S between 34.46-34.62, and Chl-*a* values between 0.98-3.02 mg m^{-3} (Fig. 7b). The pacific sampling stations included carnivore species (*O. catus*, *E. longicornis*, and *O. plumifera*,) and correlated with a wide range of S (34.36-34.65), Chl-*a* (1.0-4.34 mg m^{-3}) and DO (1.23-3.27 mL L^{-1}).

DISCUSSION

The Multivariate El Niño Index (MEI.v2) recorded significant SST anomalies from November 2014 to May 2016, reaching +0.7°C in composite MAM (March-April-May) 2015 (Coria-Monter et al. 2019, Climate Prediction Center Internet 2023). The above promoted warmer conditions (>27°C), the lack of evidence of California Current's presence in April 2015 at the CMP, and the stratification of the water column by the presence of TSW, StSsW, and TW, consistent with a seasonal intensification of the MCC in the region (Pantoja et al. 2012, Gómez-Valdivia et al.

Table 2. Summary of similarity percentage analysis (SIMPER) made on the copepod communities of the Central Mexican Pacific without the dominant and abundant copepod species. The shaded area represents copepod species contributing >80% to group dissimilarity. S%: similarity percentage, C%: contribution percentage, A%: cumulative percentage, N: number of species. The species acronyms are shown in Table 1.

Dissimilarity between groups (%)	North and south	72.19						
	North and pacific	67.05						
	South and pacific	72.02						
North			Pacific			South		
S%	46.27		S%	39.38		S%	35.12	
N	27		N	23		N	29	
Species	C%	A%	Species	C%	A%	Species	C%	A%
Ssubt	25.05	25.05	Ocat	24.09	24.09	Cmir	15.45	15.45
Pabd	15.01	40.05	Lacu	17.08	41.17	Uvul	9.67	25.12
Codar	10.5	50.56	Ssubt	12.78	53.95	Abra	8.54	33.66
Lacu	8.81	59.37	Ccra	11.64	65.59	Emar	8.51	42.16
Cmir	8.07	67.43	Elon	7.85	73.44	Cncat	8.28	50.44
Ssca	5.61	73.04	Cmir	3.95	77.39	Codar	7.76	58.2
Cqua	5.07	78.12	Oplu	3.33	80.72	Smet	7.61	65.81
Ppar	4.62	82.73	Emar	2.87	83.59	Elon	7.45	73.27
Rnas	4.3	87.03	Uvul	2.8	86.39	Scte	5.53	78.8
Elon	2.88	89.92	Pabd	2.75	89.14	Cqua	4.89	83.69
Ccra	1.91	91.83	Nmin	2.61	91.75	Ocat	3.09	86.78
						Cpav	2.45	89.23
						Ssca	1.98	91.22

Table 3. Canonical correspondence analysis of the copepod community and the environmental variables recorded at the Central Mexican Pacific (April 2015). Bold numbers: significant correlations.

Axes	1	2	3
Eigenvalues	0.123	0.080	0.044
Correlations			
Species-environment:	0.772	0.717	0.676
Accumulate variance (%)			
Species abundance	5.9	9.8	12
Species-environment	44.4	**73.4**	89.4
Environment variables			
Temperature (ºC)	0.2255	0.2893	0.2611
Salinity (S)	**-0.3652**	-0.3380	-0.3780
Dissolved oxygen (mL L^{-1})	**0.4803**	-0.0200	-0.1888
Chlorophyll-*a* concentration (mg m^{-3})	-0.1141	**0.6848**	-0.1596

2015, Portela et al. 2016, Pelayo-Martínez et al. 2017, Santana-Vega et al. 2018). The MCC carries high salinity and low oxygen concentration in the water (StSsW) into the CMP also during other seasons of the year (Kozak et al. 2014, Gómez-Valdivia et al. 2015); during April 2015, the salinity recorded in the CMP was in the range recorded by Portela et al. (2016) for spring (April-June) and fall (October-December) associated with TSW influx and periods when evaporation exceeds precipitation. These conditions also promoted the upper limit of the OMZ, reaching 40-50 m depth along the CMP related to the depth of the StSsW. At the same time, oxycline was associated with the TW distribution, supporting previous studies (Cepeda-Morales et al. 2009, 2013, Santana-Vega et al. 2018).

The water masses (TSW and StSsW) and the water transport by the MCC to the CMP generate a predominant homogenization of the area in a latitudinal sense and a tropical environment (Kozak et al. 2014, INAPESCA 2015). Local processes such as river runoff and mesoscale processes like upwellings, filaments,

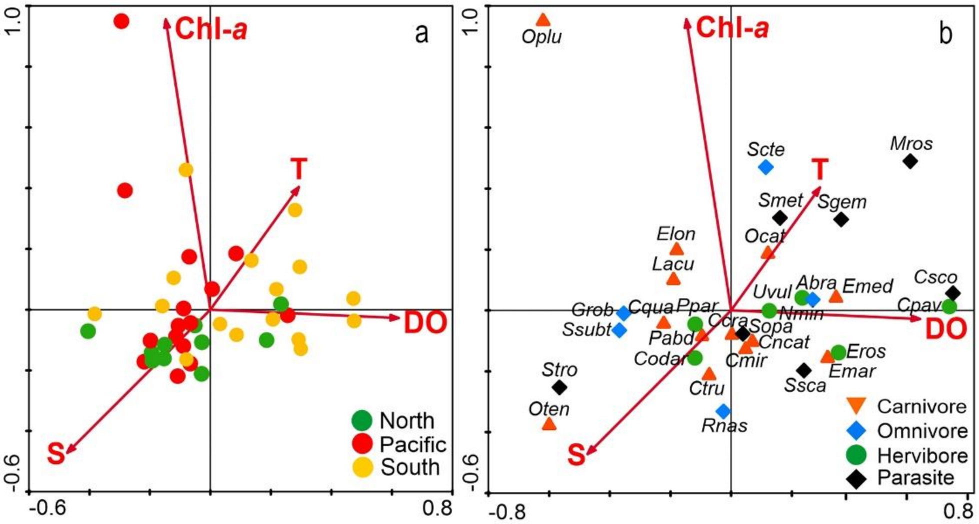

Figure 7. Canonical correspondence analysis biplots of the abundance of the copepod community (without dominant and abundant species) as a function of the environmental gradients recorded in the Central Mexican Pacific during 2015. a) Sampling stations and environmental variables showing the two-way cluster analysis groups in colors. b) Species and environmental variables showing the functional feeding groups in colors. T: temperature, S: salinity, DO: dissolvent oxygen, Chl-*a*: chlorophyll-*a* concentration. Acronyms for the species are shown in Table 1.

and eddies could favor the temperature decrease and mixing of the water column as previous records in the area (Kozak et al. 2014, Pelayo-Martínez et al. 2017, Campos-Gonzales 2018, Santana-Vega et al. 2018). The surface thermal differences between the northern and southern regions observed in satellite images show how quickly these processes occur. These environmental changes may determine differences in zooplankton communities with short life cycles, such as copepods, evidencing the rapid homogenization of the system and how local pulses of coastal productivity tend to shift, transporting high concentrations of Chl-*a* into the adjacent oceanic zone.

Latitudinally, the region off Cabo Corrientes in Jalisco has intense coastal upwellings and high productivity in spring (Campos-Gonzales 2018, Santana-Vega et al. 2018). This high regional productivity was also recorded in April 2015. The T2 recorded the maximum surface Chl-*a* in the northern zone, probably because it was located on the edge of a cyclonic eddy, inferred from the satellite imagery of SST and Chl-*a* and the elevation of isotherms in the water column (Figs. 3a-b, 4a). However, maximum subsurface Chl-*a* was recorded in Michoacan (T6) and Guerrero (T10); in Michoacan, high Chl-*a* concentrations were associated with a cold-water core (24°C isotherm), possibly related to the change in coastal physiography that promoted a widening of the productive coastal area and is the frontal zone where thermal differentiation between the northern and southern zones of the CMP occurred (Filonov & Konyaev 2003, Filonov 2011, Almazán-Becerril et al. 2012, Cepeda-Morales et al. 2017). In Guerrero, the surface filament of high Chl-*a* detached from the coast at the end of the cruise, which may be related to the transport effect of the Tehuano winds that strongly influence the Guerrero coasts (Aguirre-Gómez & Salmerón-García 2007, Reyes-Hernández et al. 2016, Coria-Monter et al. 2019).

Previous studies on the copepod community that covered areas as wide as the Eastern Tropical Pacific and more restricted from Jalisco to Colima recorded spatial and seasonal significant differences in copepod abundances (Kozak et al. 2014, López-Ibarra et al. 2014) regarding those obtained in this study in the CMP. Despite the above, the total abundances recorded in the CMP coincide with the intervals (62,681 to 47,096 ind 1000 m^{-3}) recorded in those studies and the dominance of *S. subcrassus* and *C. furcatus*. In contrast, the copepod community recorded in the CMP (our study) represents only 30% of the total species recorded for the entire Mexican Pacific reported by Hernández-Trujillo & Esqueda-Escárcega (2002), while the CMP copepod community represents 36% of the total species recorded only in previous coastal studies (Siordia-Cermeño et al. 2003, Kozak et al. 2013, 2014, López-Ibarra et al. 2014, Rojas-Herrera et al. 2016). The differences recorded in copepod communities in the CMP are determined by factors such as 1) the effect of deeper and longer hauls that generally collect larger zooplankton biovolumes and, therefore, a richer and more diverse copepod community performed in other studies (Kozak et al. 2014), 2) the collection of nocturnal biovolumes that tend to be larger due to vertical migration and displacement to the surface of the deep scattering layer (Holliland et al. 2012, Pelayo-Martínez et al. 2017), or 3) the use of differential mesh size, which determines the collection of different stages of life (nauplii-adult) or different sizes (Holliland et al. 2012) among others, besides the temporality of the study and the extension of the geographical area analyzed that may include species of different biogeographic affinities, all part of the methodologies used in the studies of copepods in the along the entire Mexican Pacific.

The uniformity of the environmental conditions in most of the sampling stations and the tropical character of the CMP determined, to a greater extent, the statistical homogeneity of the ecological indices estimated using the totality of the identified species. However, the diversity range (H' = 3.01-4.0 bits ind^{-1}) in the CMP was higher than the range of 2.9-3.0 bits ind^{-1} recorded by López-Ibarra et al. (2014), which comprised a larger study area and the Gulf of California, as well as mainly oceanic sampling stations with more saline GCW (T >12°C, S >35.1) and with a subtropical biota (Palomares-García et al. 2013, Kozak et al. 2014). In the CMP the highest diversity values, recorded at stations with the highest subsurface Chl-*a* concentrations (Michoacan T6 and Guerrero T10), suggest that the presence and effect of mesoscale enrichment processes (Aguirre-Gómez & Salmerón-García 2007, López-Sandoval et al. 2009b, Gamero-Mora et al. 2015, Reyes-Hernández et al. 2016, Pelayo-Martínez et al. 2017, Santana-Vega et al. 2018), influence the increase in regional copepod diversity through nutrient incorporation and the development of phytoplankton populations (Fernández-Álamo et al. 2000, Kozak et al. 2014, López-Ibarra et al. 2014) in which copepods feed.

Another environmental factor affecting copepods, in terms of the different feeding strategies, was the warming effect of El Niño 2014-2015 because it promoted a tropical-subtropical copepod community with mainly omnivorous and carnivorous species, comprising *Subeucalanus subcrassus*, *S. mucronatus*, *C. furcatus*, *Oithona setigera*, and *Acrocalanus gibber*. There was no increase in species richness related to the influence of El Niño 2014-2015, compared to El Niño 1997-98 for copepods and other groups of zooplankton in the oceanic zone of the Baja California Peninsula (Lavaniegos-Espejo et al. 2002), in Magdalena Bay, Baja California Sur (Palomares-García et al. 2003), and off the coast of Jalisco (Kozak et al. 2014, 2018), suggesting that the response of the tropical neritic copepod community of the CMP differs from other zooplankton groups and that the copepod community is more stable, as manifested in the diversity values, which indicate a more structured and homogeneous community. In contrast, two distinct copepod communities (analyzing all species registered) were recorded at Cabo Pulmo, located north of CMP, during the anomalous El Niño 2014-2015 event. Three small copepods, *Oncaea venusta*, *Paracalanus parvus*, and *Clausocalanus jobei*, out of 45 species, numerically dominated during 2014, while the large copepods *S. subtenuis* and *S. subcrassus* out of 38 species increased in abundance during 2015. The Cabo Pulmo community interannual differences were also observed as an increase in the abundance of subtropical and tropical species in 2015 relative to 2014 (Beltrán-Castro et al. 2020).

Although nearly all copepods are omnivorous and calanoid copepods are primarily feed current scanners, many prefer carnivory or herbivory; therefore, they are presented as such. According to Benedetti et al. (2016, 2018), the dominant species of the genus *Subeucalanus* recorded in the CMP are omnivorous and feed current scanners, while *C. furcatus* has mixed feeding strategies. Before this classification, *S. subcrassus* was described as herbivorous, *S. mucronatus* as a coarse filter feeder, and *C. furcatus* as omnivorous according to Itoh's mandibles size index (Itoh 1970, Razouls et al. 2005-2022). A decade after, other studies determined that most calanoid copepods have selective feeding from the feeding currents (Koehl & Strickier 1981, Paffenhöfer et al. 1982, Kleppel 1993). Meanwhile, Kozak et al. (2014, 2020) and López-Ibarra et al. (2014, 2018) mention that the species of the genera *Subeucalanus* and *Centropages* have a wide dietary plasticity that allows them to occupy different trophic niches (omnivorous-herbivorous) depending on the food availability. The high abundance, dominance, and wide distribution in the CMP and the entire Mexican Pacific (Siordia-Cermeño et al. 2003, López-Ibarra et al. 2014, 2018) determines that these species play an important role in the energy transfer from photoautotrophs to higher trophic levels and in the microbial food web as smaller copepods are also consuming protozoans.

The exclusion of the dominant and abundant species from our statistical analyses allowed us to determine latitudinal differences in the underlying community structure of the copepods and to relate them to the presence of mesoscale physical (upwelling to the north) and biological (subsurface maxima of Chl-*a*) processes of the south and probably to the rapid change in environmental conditions (T and Chl-*a*) recorded at the beginning and end of the oceanographic campaign observed in satellite images, which were coincident with the presence of different latitudinally distributed functional feeding groups. In these analyses, the food preferences of most copepod species recorded along the pacific group were towards carnivory and omnivory (85%). In the north, where the maximum copepod abundance was recorded, the low T, high S, and the mixing of the water column favored mostly omnivorous species because of the mesoscale eddy influence, already registered in April by Pantoja et al. (2012) and Portela et al. (2016). Also, Fernández-Álamo & Färber-Lorda (2006) established that dominance of carnivorous and omnivorous species in the water column is due to the wide and deep distribution of calanoid copepods and that herbivorous species tend to be restricted to the Chl-*a*-rich layer, which is in agreement with our findings of abundant herbivores in the Jalisco and Colima areas at Chl-*a* values of 5.0-7.0 mg m^{-3} at 20-40 m depth. In the south, the increase of herbivores and parasites was probably related to the subsurface Chl-*a* maxima (19 mg m^{-3}, from surface to 40 m depth) and a less saline and richer DO environment.

The CCA showed an environmental gradient, where the T did not play a dominant role in the distribution of copepods during April 2015, but of DO and S, together with the Chl-*a*. This analysis supports the two-way cluster analysis and the SIMPER results. Together, it determines the separation of different copepod communities distributed at the extremes of the CMP (north and south) differentiated by the structure; the species present exclusively in those areas, and their predominant functional groups. In this manner, the north zone of the CMP was characterized by a high codominance of omnivorous and carnivorous species, given by the highest abundances of *S. subtenuis* (omnivorous) and *P. abdominalis* (carnivorous), together with *P. parvus* (herbivorous) and *R. nasutus* (omnivorous) exclusively distributed in this zone, all of them associated to upwelling processes, low T in the water column, low S, and also to the presence of high zooplankton biovolumes (Cabrera-Nuñez 2018). On the contrary, the southern zone of the CMP was characterized by a higher specific diversity of carnivorous species with high abundances of *C. mirabilis* and the increase in herbivorous included *U. vulgaris* and *C. pavo*, together with more parasitic species such as *S. metallina* and *M. rosea* and another three species exclusively distributed in this area. The maximum subsurface Chl-*a* concentrations recorded along the water column in the south zone and the maximum values of DO despite the high surface T recorded explain the contrasting composition of this community compared with that of the north.

CONCLUSIONS

In the CMP of April 2015, warm conditions (mean SST >27°C), water column stratification and the presence of TSW, StSsW, and TW, and no evidence of the CCW, consistent with a seasonal intensification of the MCC under El Niño 2014-2015 conditions were recorded, which determined that community attributes (abundance, species richness, diversity, dominance) did not register significant differences along the CMP. The copepod community recorded in the CMP represents only 30% of the total species recorded for the entire Mexican Pacific and 36% of the total species recorded in previous coastal studies. The copepods community showed a statistically homogeneous community structure due to the dominance and wide distribution of *S. subcrassus*, *C. furcatus*, and *S. mucronatus*, key copepod species in the area. By extracting the dominant and abundant species from the analysis, significant latitudinal differences in the underlying community structure were detected, which was also reflected in a difference in their predominant functional feeding strategy in the north and south zones. The in-depth analysis of the copepod community of the CMP considering their underlying structure was a useful tool that allowed to establish clear north and south differences related not to a T environmental gradient but to DO, S, and Chl-*a* and to the influence of local mesoscale processes (eddies, jets, upwelling) in an area traditionally considered very homogeneous throughout the year. The copepod species studied here represent a key part of the zooplankton community, useful to know and understand the status of the pelagic environment in the marine ecosystem and in the CMP under anomalously warm conditions of El Niño 2014-2015, as well as for being a trophic link that connects primary producers with consumers of higher levels, like its function in the northern portion of the Mexican Pacific.

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REFERENCES

Administración Nacional de Aeronáutica y el Espacio (NASA). 2023a. SST, Aqua MODIS, NPP, 0.025 degrees, Pacific Ocean, Daytime, 2006-present (5 Day Composite), Lon+/-180, NOAA NMFS SWFSC ERD. [https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMBsstd8day_LonPM180.graph]. Reviewed: October 10, 2019.

Administración Nacional de Aeronáutica y el Espacio (NASA). 2023b. Chlorophyll, NOAA S-NPP VIIRS, Science Quality, Global 4km, Level 3, 2012-present, Weekly. NOAA NESDIS CoastWatch. [https://coastwatch.pfeg.noaa.gov/erddap/info/nesdisVHNSQchlaWeekly/index.html]. Reviewed: October 10, 2019.

Aguirre-Gómez, R. & Salmerón-García, O. 2007. Análisis estacional de la variación en la clorofila en el Pacífico Sur Mexicano mediante imágenes SeaWIFS de 1998 a 2004. In: Hernández, B. & Gaxiola, C.G. (Eds.). Carbono en ecosistemas acuáticos de México. Instituto Nacional de Ecología y Cambio Climático, México DF, pp. 267-278.

Almazán-Becerril, A., Rivas, D. & García-Mendoza, E. 2012. The influence of mesoscale physical structures in the phytoplankton taxonomic composition of the subsurface chlorophyll maximum off western Baja California. Deep Sea Research Part I, 70: 91-102. doi: 0.1016/j.dsr.2012.10.002

Ambriz-Arreola, I., Gómez-Gutiérrez, J., Franco-Gordo, M.C., Lavaniegos, B.E. & Godínez-Domínguez, E. 2012. Influence of coastal upwelling-downwelling variability on tropical euphausiid abundance and community structure in the inshore Mexican central Pacific. Marine Ecology Progress Series, 451: 119-136. doi: 10.3354/meps09607

Beltrán-Castro, J.R., Hernández-Trujillo, S., Gómez-Gutiérrez, J., Trasviña-Castro, A., González-Rodríguez, E. & Aburto-Oropeza, O. 2020. Copepod species assemblage and carbon biomass during two anomalous warm periods of distinct origin during 2014-2015 in the southern Gulf of California. Continental Shelf Research, 207: 104215. doi: 10.1016/j.csr.2020.104215

Benedetti, F., Gasparini, S. & Ayata, S.-D. 2016. Identifying copepod functional groups from species functional traits. Journal of Plankton Research, 38: 159-166. doi: 10.1093/plankt/fbv096

Benedetti, F., Vogt, M., Righetti, D., Guilhaumon, F. & Ayata, S.D. 2018. Do functional groups of planktonic copepods differ in their ecological niches? Journal of Biogeography, 45: 604-616. doi: 10.1111/jbi.13166

Cabrera-Nuñez, S. 2018. Estructura de la comunidad del zooplancton en la zona costera del Pacífico central mexicano (abril 2015). Master Thesis, Instituto Politécnico Nacional, La Paz.

Camarillo-Coop, S., Salinas-Zavala, C.A., Lavaniegos, B.E. & Markaida, U. 2013. Food in early life stages of *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. Journal of the Marine Biological Association of the United Kingdom, 93: 1903-1910. doi: 10.1017/S0025315413000398

Campos-Gonzales, F.E. 2018. Propiedades de los remolinos de mesoescala al sur de Baja California: un análisis numérico. Master Thesis, Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California.

Cepeda-Morales, J., Gaxiola-Castro, G., Beier, E. & Godínez, V.M. 2013. The mechanisms involved in defining the northern boundary of the shallow oxygen minimum zone in the eastern tropical Pacific Ocean off Mexico. Deep-Sea Research - Part I, 76: 1-12. doi: 10.1016/j.dsr.2013.02.004

Cepeda-Morales, J., Beier, E., Gaxiola-Castro, G., Lavín, M.F. & Godínez, V.M. 2009. Effect of the oxygen minimum zone on the second chlorophyll maximum in the Eastern Tropical Pacific off Mexico. Ciencias Marinas, 35: 389-403. doi: 10.7773/cm.v35i4.1622

Cepeda-Morales, J., Hernández-Vásquez, F., Rivera-Caicedo, J., Romero-Bañuelos, C., Inda-Díaz, E. & Hernández-Almeida, O. 2017. Seasonal variability of satellite-derived chlorophyll and sea surface temperature on the continental shelf of Nayarit, Mexico. Revista Bio Ciencias, 4: 1-17. doi: 10.15741/revbio.04.06.07

Climate Prediction Center Internet. 2023. Historical El Niño/La Niña episodes (1950-present). NOAA/National Weather Service National Centers for Environmental Prediction. [https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php]. Reviewed: March 26, 2023.

Comisión Nacional de Áreas Naturales Protegidas (CONANP). 2018. Programa de manejo reserva de la biosfera Pacífico mexicano profundo. SEMARNAT-CONANP, Mexico DF.

Coria-Monter, E., Salas de León, D.A., Monreal-Gómez, M.A. & Durán-Campos, E. 2019. Satellite observations of the effect of the "Godzilla El Niño" on the Tehuantepec upwelling system in the Mexican Pacific. Helgoland Marine Research, 73: 3. doi: 0.1186/s 10152-019-0525-y

Daly, A.J., Baetens, J.M. & De Baets, B. 2018. Ecological diversity: measuring the unmeasurable. Mathematics, 6: 119. doi: 10.3390/math6070119

De Silva-Dávila, R., Franco-Gordo, C., Hochberg, F.G., Godínez-Domínguez, E., Avendaño-Ibarra, R., Gómez-Gutiérrez, J. & Robinson, C.J. 2015. Cephalopod paralarval assemblages in the Gulf of California during 2004-2007. Marine Ecology Progress Series, 520: 123-141. doi: 10.3354/ meps11074

Fernández-Álamo, M.A. & Färber-Lorda, J. 2006. Zooplankton and the oceanography of the Eastern tropical Pacific: a review. Progress in Oceanography, 69: 318-359. doi: 10.1016/j.pocean.2006.03.003

Fernández-Álamo, M.A., Sanvicente-Añorve, L. & Alameda-de-la-Mora, G. 2000. Copepod assemblages in the Gulf of Tehuantepec, Mexico. Crustaceana, 73: 1139-1153. doi: 10.1163/156854000505137

Filonov, A. 2011. Inclined internal tide waves at a narrow Mexican Pacific shelf. Ocean Dynamics, 61: 917-931. doi: 10.1007/s10236-011-0409-4

Filonov, A.E. & Konyaev, K.V. 2003. Nonlinear internal waves near Mexico's central Pacific coast. In: Velasco-Fuentes, O.U., Sheinbaum, J. & Ochoa, J. (Eds.). Nonlinear processes in geophysical fluid dynamics. Kluwer Academic Publishers, Amsterdam, pp. 377-386.

Gael, D., Jiang-Shiou, H., Sami, S., Li-Chun, T., Cheng-Han, W., Shih-Hui, H., et al. 2007. An overview of the influence of hydrodynamics on the spatial and temporal patterns of calanoid copepod communities around Taiwan. Journal of Plankton Research, 29: 97-116. doi: 10.1093/plankt/fbl070

Gamero-Mora, E., Ceballos-Corona, G., Gasca, R. & Morales-Blake, A. 2015. Análisis de la comunidad del zooplancton gelatinoso (Hydrozoa, Ctenophora, Thaliacea) en el Pacífico central mexicano, abril-mayo 2011. Revista de Biología Marina y Oceanografía, 50: 111-124. doi: 10.4067/S0718-19572015000100009

Gómez-Valdivia, F., Parés-Sierra, A. & Flores-Morales, A.L. 2015. The Mexican Coastal Current: a subsurface seasonal bridge that connects the tropical and subtropical Northeastern Pacific. Continental Shelf Research, 110: 100-107. doi: 10.1016/j.csr.2015.10.010

Hendrickx, M.E. & Serrano, D. 2010. Impacto de la zona de mínimo de oxígeno sobre los corredores pesqueros en el Pacífico Mexicano. Interciencia, 35: 12-18.

Hernández-Trujillo, S. & Esqueda-Escárcega, G.M. 2002. La diversidad de copépodos marinos en México. Oceánides, 17: 57-68.

Hernández-Trujillo, S., Esqueda-Escárcega, G.M. & Palomares-García, R. 2010. Variabilidad de la abundancia de zooplancton en Bahía Magdalena Baja California Sur, México (1997-2001). Latin American Journal of Aquatic Research, 38: 438-446. doi: 10.3856/vol38-issue3-fulltext-8

Holliland, P.B., Ahlbeck, I., Westlund, E. & Hansson, S. 2012. Ontogenetic and seasonal changes in diel vertical migration amplitude of the calanoid copepods *Eurytemora affinis* and *Acartia* spp. in a coastal area of the northern Baltic proper. Journal of Plankton Research, 34: 298-307. doi: 10.1093/plankt/fbs001

Instituto Nacional de la Pesca (INAPESCA). 2015. Boletín hidroclimático de los mares de México: temperatura superficial del mar: Abril 2015. INAPESCA. [https://www.inapesca.gob.mx/portal/documentos/publicaciones/BOLETINES/hidroclimatico/TEMPERATURA/boletin-hidrometeorologico-abril-2015-temperatura-2.pdf]. Reviewed: April 5, 2022.

Itoh, K. 1970. A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts. Bulletin of Plankton Society of Japan, 17: 1-10.

Kleppel, G.S. 1993. On the diets of calanoid copepods. Marine Ecology Progress Series, 99: 183-195.

Koehl, M.A.R. & Strickier, J.R. 1981. Copepod feeding currents: food capture at low Reynolds number[1]. Limnology and Oceanography, 26: 1062-1073. doi: 10.4319/lo.1981.26.6.1062

Kozak, E.R., Franco-Gordo, M.C., Suárez-Morales, E. & Palomares-García, R. 2014. Seasonal and interannual variability of the calanoid copepod community structure in shelf waters of the Eastern Tropical Pacific. Marine Ecology Progress Series, 507: 95-110. doi: 10.3354/meps10811

Kozak, E.R., Olivos-Ortiz, A., Franco-Gordo, C. & Pelayo-Martínez, G. 2018. Seasonal variability of copepod community structure and abundance modified by the El Niño-La Niña transition (2010), Pacific, Mexico. Revista de Biología Tropical, 66: 1449-1468. doi: 10.15517/rbt.v66i4.32058

Kozak, E.R., Suárez-Morales, E., Palomares-García, R. & Franco-Gordo, M.C. 2013. Copépodos de la costa sur de Jalisco y Colima. In: Franco-Gordo, M.C. (Ed.). Inventario de biodiversidad de la costa sur de Jalisco y Colima. Vol. I. Universidad De Guadalajara, Guadalajara, pp. 79-91.

Kozak, E.R., Franco-Gordo, C., Godínez-Domínguez, E., Suárez-Morales, E. & Ambriz-Arreola, I. 2020. Seasonal variability of stable isotope values and niche size in tropical calanoid copepods and zooplankton size fractions. Marine Biology, 167: 37. doi: 10.1007/s00227-020-3653-7

Kramer, D., Kalin, J.M., Stevens, G.E., Thrailkill, R.J. & Zweifel, R.J. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA technical report NMFS CIRC, 370. [https://repository.library.noaa.gov/view/noaa/3248]. Reviewed: May 20, 2018.

Lavaniegos-Espejo, B., Jiménez-Pérez, L.C. & Gaxiola-Castro, G. 2002. Plankton response to El Niño 1997-1998 and La Niña 1999 in the southern region of the California Current. Progress in Oceanography, 54: 33-58. doi: 10.1016/S0079-611(02)00042-3

Lavín, M.F., Beier, E., Gómez-Valdés, J., Godínez, V.M., & García, J. 2006. On the summer poleward coastal current off SW México. Geophysical Research Letters, 33: L02601. doi: 10.1029/2005GL024686

Legendre, P. & Legendre, L. 2012. Cluster analysis. In: Legendre, P. & Legendre, L. (Eds.). Developments in environmental modelling. Elsevier, Amsterdam, pp. 337-424.

Longhurst, A.R. 1985. The structure and evolution of plankton communities. Progress in Oceanography, 15: 1-35. doi: 10.1016/0079-6611(85)90036-9

López-Ibarra, G.A., Hernández-Trujillo, S., Bode, A. & Zetina-Rejón, M.J. 2014. Community structure of pelagic copepods in the eastern tropical Pacific Ocean during summer and autumn. Cahiers de Biologie Marine, 55: 453-462.

López-Ibarra, G.A., Bode, A., Hernández-Trujillo, S., Zetina-Rejón, M.J. & Arreguin-Sánchez, F. 2018. Trophic position of twelve dominant pelagic copepods in the eastern tropical Pacific Ocean. Journal of Marine Systems, 187: 13-22. doi: 10.1016/j.jmarsys.2018.06.009

López-Sandoval, D.C., Lara-Lara, J.R., Álvarez-Borrego, S. 2009a. Phytoplankton production by remote sensing in the region off Cabo Corrientes, Mexico. Hidrobiológica, 19: 185-192.

López-Sandoval, D.C., Lara-Lara, J.R., Lavín, M.F., Álvarez-Borrego, S. & Gaxiola-Castro, G. 2009b. Primary productivity observations in the eastern tropical Pacific off Cabo Corrientes, Mexico. Ciencias Marinas, 35: 169-182. doi: 10.7773/cm.v35i2.1530

Martínez-Soler, E., Gómez-Gutiérrez, J., De Silva-Dávila, R., González-Rodríguez, E. & Aburto-Oropeza, O. 2021. Cephalopod paralarval species richness, abundance, and size structure during the 2014-2017 anomalous warm period in the southern Gulf of California. Journal of Plankton Research, 43: 224-243. doi: 10.1093/plankt/fbab010

Maske-Rubach, H., Hernández-Ayón, J.M. & Beier, E.J. 2017. Aguas oceánicas subsuperficiales sin oxígeno, pero abundantes en carbono inorgánico y nutrientes frente a las costas del Pacífico de México. Elementos para Políticas Públicas, 1: 25-34.

McCune, B. & Mefford, M.J. 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0. MjM Software Design, Gleneden Beach.

Ostertagová, E., Ostertag, O. & Kováč, J. 2014. Methodology and application of the Kruskal-Wallis test. Applied Mechanics and Materials, 611: 115-120. doi: 10.4028/www.scientific.net/amm.611.115

Paffenhöfer, G.A., Strickler, J.R. & Alcaraz, M. 1982. Suspension-feeding by herbivorous calanoid copepods: a cinematographic study. Marine Biology, 67: 193-199. doi: 10.1007/BF00401285

Palomares-García, R.J. & Vera-Alejandre, R. 1995. Predation upon larvae of the Pacific sardine *Sardinops sagax* by cyclopoid copepods. Journal of Crustacean Biology, 15: 196-201. doi: 10.2307/1549021

Palomares-García, R.J., De Silva-Dávila, R. & Avendaño-Ibarra, R. 2018. Depredación de copépodos sobre paralarvas del complejo *Sthenoteuthis oualaniensis-Dosidicus gigas* en el Golfo de California. In: Pérez-Morales, A. & Álvarez-García, M.C. (Eds.). Estudios recientes en el Océano Pacífico mexicano. Universidad de Colima, Colima, pp. 43-61.

Palomares-García, R.J., Gómez-Gutiérrez, J. & Robinson, C.J. 2013. Winter and summer vertical distribution of epipelagic copepods in the Gulf of California. Journal of Plankton Research, 35: 1009-1026. doi: 10.1093/plankt/fbt052

Palomares-García, R., Suárez-Morales, E. & Hernández-Trujillo, S. 1998. Catálogo de los copépodos (Crustacea) pelágicos del Pacífico Mexicano. CICIMAR-IPN-ECOSUR, La Paz.

Palomares-García, R.J., Martínez-Lopéz, A., De Silva-Dávila, R., Funes-Rodríguez, R., Carballido-Carranza, M.A., Avendaño-Ibarra, A, et al. 2003. Biological effects of El Niño 1997-98, in a shallow subtropical ecosystem: Bahía Magdalena, Mexico. Geofísica Internacional, 42: 455-466.

Pantoja, D.A., Marinone, S.G., Parés-Sierra, A. & Gómez-Valdivia, F. 2012. Numerical modeling of seasonal and mesoscale hydrography and circulation in the Mexican Central Pacific. Ciencias Marinas, 38: 363-379. doi: 10.7773/cm.v38i2.2007

Peck, J.E. 2010. Multivariate analysis for community ecologists. Step-by-Step using PC-ORD. MjM Software Design, Gleneden Beach.

Pelayo-Martínez, G., Olivos-Ortiz, A., Franco-Gordo, C., Quijano-Scheggia, S., Gaviño-Rodríguez, J., Kono-Martínez, T., et al. 2017. Physical, chemical, and zooplankton biomass variability (inshore-offshore) of Mexican Central Pacific during El Niño-La Niña 2010. Latin American Journal of Aquatic Research, 45: 67-78. doi: 10.3856/vol45-issue1-fulltext-7

Portela, E., Beier, E., Barton, E.D., Castro, R., Godínez, V., Palacios-Hernández, E., et al. 2016. Water masses and circulation in the Tropical Pacific off Central Mexico and surrounding areas. Journal of Physical Oceanography, 46: 3069-3081. doi: 10.1175/JPO-D-16-0068.1

Razouls, C., Desreumaux, N., Kouwenberg, J. & De Bovée, F. 2005-2022. Biodiversity of marine planktonic copepods (morphology, geographical distribution and biological data). Sorbonne University, Paris. [http://copepodes.obs-banyuls.fr/en]. Reviewed: June 2, 2022.

Reyes-Hernández, C., Ahumada-Sempoal, M.A. & Durazo, R. 2016. The Costa Rica Coastal Current, eddies and wind forcing in the Gulf of Tehuantepec, Southern Mexican Pacific. Continental Shelf Research, 114: 1-15. doi: 10.1016/j.csr.2015.12.012

Rojas-Herrera, A.A., Violante-González, J., García-Ibáñez, S., Villerías-Salinas, S. & Moreno-Díaz, G. 2016. Temporal variation of the pelagic copepod community in Acapulco Bay, México. Open Journal of Marine Science, 6: 40-48. doi: 10.4236/ojms.2016.61005

Santana-Vega, Z., Hernández-Becerril, D.U., Morales-Blake, A.R., Varona-Cordero, F. & Merino-Ibarra, M. 2018. Prokaryotic picoplankton distribution within the oxygen minimum zone of the central Mexican Pacific across environmental gradients. Brazilian Journal of Oceanography, 66: 157-171. doi: 10.1590/s1679-8759 2018004806602

Sea-Bird Scientific. 2017. Software Manual. Seasoft V2: SBE Data processing. [https://www.seabird.com/eBooks#]. Reviewed: March 16, 2023.

Siordia-Cermeño, M.P., Sánchez-Velasco, L., Franco-Gordo, M.C. & Sánchez-Ramírez, M. 2003. Variación temporal del zooplancton, con énfasis en crustáceos, en las costas de Jalisco y Colima durante un ciclo anual (1996). In: Hendrickx, M.E. (Ed.). Contribuciones al estudio de los crustáceos del Pacífico Este. UNAM, México DF, pp. 93-101.

Suárez-Morales, E., Franco-Gordo, C. & Saucedo-Lozano, M. 2000. On the pelagic copepod community of the central Mexican tropical Pacific (Autumn, 1990). Crustaceana, 73: 751-761.

Uchikawa, K., Sakai, M., Wakabayashy, T. & Ichii, T. 2009. The relationship between paralarval feeding and morphological changes in the proboscis and beaks of the neon flying squid *Ommastrephes bartramii*. Fishery Science, 75: 317-323. doi: 10.1007/s12562-008-0036-2

Venelleo, T.A., Sastri, A.R., Galbraith, M.D. & Dower, J.F. 2021. Zooplankton functional group responses to environmental drivers off the west coast of Vancouver Island, Canada. Progress in Oceanography, 190: 102482. doi: 10.1016/j.pocean.2020.102482

Walter, T.C. & Boxshall, G. 2022. World of copepods database. World Register of Marine Species. [http://www.marinespecies.org/index.php]. Reviewed: June 3, 2022.

Wilkinson, T., Wiken, E., Bezaury-Creel, J., Hourigan, T., Agardy, T., Herrmann, H., et al. 2009. Ecorregiones marinas de América del Norte. Comisión para la Cooperación Ambiental, Montreal.

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