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Richness and diversity of pelagic copepods at two stations ten miles off the coast of Ecuador

Riqueza y diversidad de copépodos pelágicos en dos estaciones a diez millas de las costas de Ecuador

Artículo

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Abstract

Among marine zooplankton organisms, copepods are the most abundant and diverse planktonic group in pelagic marine ecosystems. Therefore, the seasonal variability of epipelagic copepods was studied in two stations located 10 miles off the Ecuadorian coast from 2016 to 2019. The effect of oceanographic conditions on spatial and temporal variations in abundance, diversity and copepod richness was evaluated. Sixty-eight species belonging to the orders Calanoides, Ciclopoides, Harpacticoides and Sifonostomatoide were identified. Of these groups, *Canthocalanus pauper*, *Acrocalanus longicornis*, *Oncaea venusta* and *Centropages furcatus* were the most frequent and abundant in the entire community. Manta and La Libertad recorded 61 and 60 species, respectively, and during the wet and dry seasons 56 and 58 individuals were recorded, reciprocally, of which 50 species were common in both seasons and seasons. Temperature ranged from 22.37

to 29.16°C; salinity varied between 31.60 and 34.90 ppm and thermal anomalies fluctuated between -0.20 and +2.35°C. Significant differences were detected in the seasonal variability of the environmental and biological parameters. The Shannon-Wiener diversity (H') and species richness (DMg) indices were related to the different conditions of temperature and salinity of the sea surface, detecting higher diversity and richness in the dry season and lower in the wet season. The Principal Component and Canonical Correspondence Analysis related two groups of copepods, one group would be associated with Tropical Surface Waters and the other with Equatorial Surface Waters. The results of the research determined that the structure and dynamics of copepods in the study area were structured by seasonal water mass patterns that occurred in the Ecuadorian Pacific.

Key words: opepods, epipelagic, advection, richness index, diversity, equity.

Resumen

Dentro de los organismos el zooplancton marino, los copépodos es el grupo planctónico más abundante y diverso en los ecosistemas marinos pelágicos. Por lo que se estudió la variabilidad estacional de los copépodos epipelágicos en dos estaciones localizadas a 10 millas de la costa ecuatoriana desde el 2016 al 2019. Evaluándose el efecto de las condiciones oceanográficas sobre las variaciones espaciales y temporales de la abundancia, diversidad y riqueza copepodiana. Se identificaron 68 especies pertenecientes a los órdenes, Calanoides, Ciclopoides, Harpacticoides y Sifonostomatoide. De estos grupos *Canthocalanus pauper*, *Acrocalanus longicornis*, *Oncaea venusta* y *Centropages furcatus* fueron más frecuentes y abundantes de toda la comunidad. Manta y La Libertad se registraron 61 y 60 especies, respectivamente y durante la época húmeda y la seca se registraron 56 y 58 individuos, recíprocamente, de los cuales 50 especies fueron comunes en ambas estaciones y épocas. La temperatura osciló entre 22.37 a 29.16 °C; la salinidad, varió entre 31.60 y 34.90 ppm y las anomalías térmicas fluctuaron entre -0.20 y +2.35°C. Detectándose diferencias significativas en la variabilidad estacional de los parámetros ambientales y biológicos. Los índices diversidad de Shannon-Wiener (H') y riqueza de especies (D_{Mg}) estaban relacionados con las distintas condiciones de temperatura y salinidad de la superficie del mar, detectándose mayor diversidad y riqueza en la época seca y menor en la época húmeda. Los Análisis de Componentes Principales y de Correspondencia Canónica relacionó dos grupos de copépodos, un grupo estaría asociadas a Aguas Tropicales Superficiales y otro grupo, a Aguas Ecuatoriales Superficiales. Los resultados de la investigación, determinó que la estructura y la dinámica de los copépodos en el área de estudio estaban estructuradas por patrones de masas de aguas estacionales que se presentaron en el Pacífico ecuatoriano.

Palabras clave: copépodos, epipelágicos, advección, índice de riqueza, diversidad, equidad.

Introduction

In marine zooplankton, copepods account for 70-90% of all individuals in this group (Neumann *et al.* 2008, Zakaria *et al.,* 2016, Medellin *et al.,* 2021). Pelagic copepods are characterized by their species richness and diversity, by occupying wide variety of habitats, by their high contribution to zooplankton biomass and by the transfer of energy between primary producers to higher trophic levels (Roemmich and McGowan 1995; Beaugrand 2009, Olson *et al.,* 2010). In addition, they are involved in the transport of organic carbon to the deep ocean by excreting nutrients, which can be recycled by phytoplankton (Harris *et al.,* 2000; Valdés *et al.,* 2018). Therefore, they provide significant information about ecosystem dynamics (Spinelli *et al.,* 2016), which make them important indicators of ecosystem functioning (Campos *et al.,* 2017).

Marine systems are very dynamic, as they experience oscillations in their physical and chemical properties, oscillations that have a profound effect on biological processes, causing diversity and taxonomic richness to vary at all time scales, these variations are fundamental in the ecological processes of the ecosystem (Record *et al.,* 2010; Mann and Lazier, 2013). Some studies have shown that changes in water masses in the ocean cause interannual to decadal differences in copepod biodiversity, so they are considered excellent indicators of ocean conditions (Hooff & Peterson. 2006; Peterson. 2009).

Throughout the Eastern Tropical Pacific off South America, studies have been conducted in terms of abundance, biodiversity and spatiotemporal distribution of copepods as a function of changes in water masses. In the Colombian Pacific, Giraldo and Gutiérrez (2007), point out that oceanographic conditions at the regional level would establish the behavior for surface zooplankton to be distributed in space; López, (2012) states that the distribution of copepods is related to variations in oceanographic conditions and oceanographic at micro-, meso-macroscale and also climatic; Jaimes & López, (2014), showed that the biomass, abundance and homogeneous distribution of copepods could correspond to the physical-chemical conditions that occur in the surface layer of the sea; López & Mojica, (2015), observed, the influence of ocean currents on the distribution, transport, dispersion and/or retention of copepods at different spatial and temporal scales. In Peru, Smith *et al,* (1971) investigated the vertical distribution of Oncaeidae, Oithonidae and small Calanoides copepods, determining that these species do not migrate beyond 30 m both during the day and at night; Herman & Sameoto (1981) described the abundance, species composition and migratory patterns of several copepod species and their relationship with temperature, salinity and chlorophyll a; Criales-Hernández *et al.* (2008) showed that the abundance and distribution of communities are linked to changes in the dynamics of oxycline, which influences the vertical distribution of zooplankton in coastal waters. In Chile, Hirakawa (1989), detected the influence of sub-Antarctic surface water masses and equatorial subsurface water in Chilean fjords based on the presence of zooplankton species associated with these water masses; Escribano & Hidalgo (2000), associated the transport of zooplankton fractions to more oceanic waters to the advection process during active upwelling; Hidalgo *et al*. (2010), showed the fundamental role of upwelling in the dynamics of copepods, which would cause an increase in their diversity in the food-rich photic zone; Hidalgo *et al.* (2012), concluded that the process of coastal upwelling is an important factor in the diversity of copepods, in addition, it causes variations in the depth of the minimum oxygen zone affecting the composition of planktonic communities.

Since the study area is located in the Eastern Equatorial Pacific, the zone is influenced by two defined alternating seasonal periods. The dry season occurs from May to November, being more intense in August-September, and the rainy season occurs from December to April, with a maximum peak in February-March (Hastenrath. 2002; Koutavas and Lynch-Stieglitz, 2004; Hernández. 2006). This seasonality is associated with the north-south migration of the Intertropical Convergence Zone (ITCZ), which moves north during the dry season and south during the rainy season (Waliser and Gautier, 1993; Hernández. 2006).

Research on copepod diversity in the oligotrophic waters of the eastern Pacific indicates that species can occupy different strata in the water column according to the temperature of each stratum (Medellin *et al*. 2021). Likewise, community structure is greater in areas of influence of tropical water masses (Hernández *et al*. 2014). These processes are related to temporal variations in the hydrographic conditions of the Eastern Tropical Pacific (Jerez *et al*. 2022).

Studies conducted in the Ecuadorian Pacific indicate that plankton biodiversity is influenced by hydrological, oceanographic and seasonal processes, as well as by the interrelationships between plankton components (Prado & Cajas. 2009; Coello *et al.* 2010; Tutasi *et al.* 2011; Cajas. 2012). Martinez. 2019; Bucheli *et al.* 2019; Bucheli & Cajas. 2020).

Studies have shown the predominance of copepods in the Ecuadorian Pacific.

On the other hand, in Ecuadorian coastal waters affected by watersheds, species richness is sometimes dominated by estuarine organisms such as the copepod *Acartia lilljeborgi. Likewise,* in areas where oceanic and coastal waters are mixed without watershed influences, biodiversity is controlled by small herbivorous copepods such as *Paracalanus parvus, Oncaea clevei*, *Oncaea venusta, Oithona rigida* and *Clausucalanus furcatus* (Prado & Cajas, 2009; Coello et *al.* 2010).

In the Ecuadorian Pacific, there is little work on copepod richness and diversity, despite their ecological importance in the marine food web and as indicators of water masses. The objective of the present study is to investigate the dynamics of copepod species diversity and richness over time with respect to temporal variations in temperature and salinity, to determine the dynamics of the copepod assemblage in response to environmental conditions at two stations off the Ecuadorian coast.

Materials and Methods

Study area

During the study period from 2016-2019, monthly sampling was conducted at two stations 10 miles off the Ecuadorian coast. The study was developed in the provinces of Manabí off the coast of Manta (-0º 52' 2.2794" S; -80º 50' 4.5594" W) and Santa Elena off La Libertad (-2º 3' 53.9994" S; -81º 7' 15.5994 "W) (Figure. 1). These areas stand out for being a very productive fishing sector and because they are located in the Ecuadorian Pacific, they are influenced by several ocean currents. From the north comes a warm current, low in nutrients and low salinity, the Panama Current, which is present during the wet season, from January to April. While to the south and in a northerly direction flows a cold current rich in nutrients with high levels of salinity and chlorophyll, the Peruvian Coastal Current (Humboldt), which occurs during the dry season from July to November (Cucalón, 1989; Fiedler and Talley, 2006; Lavin *et al.,* 2006; Pennington *et al.,* 2006; Thiel *et al.,* 2007; Conde *et al.,* 2018). Likewise, two currents converge, the North Equatorial Countercurrent (NECC) and the South Equatorial Current (SEC) forming the Equatorial Front (EF) whose latitudinal position varies throughout the year. According to the information of vertical profiles of temperature, salinity, density and nutrients in the water column, the following water masses are present in the area; Tropical Surface Waters (ATS), Equatorial Surface Waters (AES), Peruvian Coastal Waters (ACP) and Equatorial Subsurface Waters (AESS); these water masses frequent Ecuadorian waters according to latitude, longitude, depth and times of the year; and some are more intense during El Niño and La Niña events (Valencia. 1996; Carrillo. 2013). The first two water masses occur from the surface level to 20 m, while the third mass occurs up to 50 m depth (Carrillo. 2013).

Sample collection

Zooplankton samples were collected once a month from a boat using a plankton net with a mouth diameter of 30 cm and a mesh size of 200 µm, preserved with 4% formaldehyde. The net worked superficially at a speed of 2 knots during 5 minutes, and for the water column from 50 m towards 0 m. The volume of filtered water was estimated according to the Sergio Frontier technique (Boltovskoy, 1981). In addition, temperature and salinity data were taken at each station from 50 m to 0 m with a conductivity-temperature-depth profiler (CTD) (CPPS. 2015).

Laboratory analysis

The analysis of the samples was carried out in the plankton laboratory of the Instituto Público de Investigación de Acuicultura y Pesca (IPIAP), where the quali-quantitative analysis of zooplankton was carried out by taking an aliquot of 25 ml, which was deposited in a Dollphus chamber, counting and identifying only the adult copepods by means of a stereoscopic microscope (LEICA 25). The estimated abundances were standardized to 1 m^3 of filtered water, applying the Sergio Frontier technique (Boltovskoy, 1981). Copepods were identified to species level using taxonomic keys of Boltovskoy (1981;1999).

Data analysis

To determine possible significant differences in hydrochemical variables at the spatial level (between stations), a non-parametric analysis of variance was performed using the Kruskal-Wallis significance test ($P<0.05$) (McKight & Najab. (2010), after applying the Kolmogorov-Smirnov normality test (Gómez *et al.* 2003) and Levene homoscedasticity (Sheskin, 2003).

Ecological diversity indices were calculated to evaluate variations in the taxonomic structure of copepods. The Shannon-Weaver (H') diversity index (Shannon and Weaver 1949) described in Franco et al. (1985) was applied. Species richness was calculated with the Margalef index (D_{Mg}) (Margalef 1958), and the evenness of samples was estimated using the Pielou Index (J') (Pielou 1969). In order to resemble the relative importance of common and rare copepod species, the data were square root transformed (Krebs 1989). Principal component analysis (PCA) (Gurrea, 2000) was applied to assess the relationships between total copepod abundance, ecological indices (H', D_{Mg} and J') and abiotic variables (temperature and salinity).

In order to understand the effect of environmental variables on the 90 species including copepodite stages, a canonical correspondence analysis (CCA) was performed (Fajardo *et al.* 2018), for which the 90 specimens were divided into group of 30 individuals (Figure 7).

Primer 7, Statgraphics 5.1 and R Studio were used for statistical analysis, and QGIS 2.18 was used for map construction.

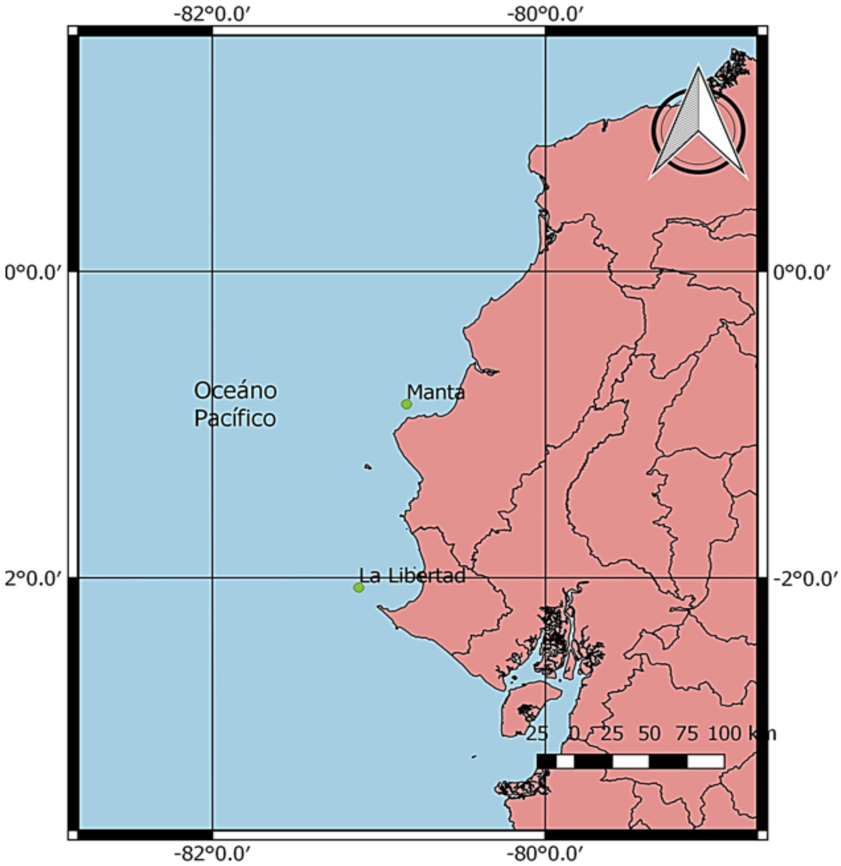


Figure 1. Position of the sampling stations in the study area.

Results

Environmental parameters

The sea surface temperature (SST) values in the study area recorded from 2016 to 2019, ranged from 22.37 to 29.16° C. The highest temperatures were recorded in the wet season of 2016, 2017 and 2019, mainly, in the months of March, April and May; high dry season temperatures were also observed during the month of June 2016, 2017 and 2019; on the contrary, 2018 was the year with the lowest SSTs, temperatures that were more evident from June to November (Figure 2a). Consequently, during the dry season, most temperatures were concentrated between 23.80 and 25.40 ° C and during the wet season, between 25.40 and 28.00° C; moreover, the conditions with the highest SST were observed in March, April and July and the lowest was recorded in September and November (Figure 3a and 3b). Significant differences ($p<0.05$) were detected between months and between seasons, with the lowest records in the dry season.

The anomalies of the sea surface temperature (ATSM), fluctuated between -0.20 ° C and +2.35. ATSM higher than +2.00°C presented in the wet season of 2017, specifically in the months of March, April and May and also in May 2016 and 2019; in the same way, thermal anomalies higher than +2.00°C in the dry season of 2016 and 2017, specifically in the months of June and July; On the other hand the lowest thermal anomalies were recorded in dry season, whose values ranged from -2.00°C to -5.00°C, being more visible during October and November 2016, in October 2017 and in June 2018 (Figure 2b). It was also observed that, during the dry season, most of the anomalies were located between 0.00 and +0.80° C and in the wet season, between +0.80 and +1.70° C; likewise, during the months of March, April and July the ranges of dispersion of the ATSMs were the widest, while in November they were the least variable. In summary, during 2016 and 2017, the highest ATSMs were detected and during 2018, the lowest ATSMs (Figure 3c and 3d). Significant differences ($p<0.05$) were detected between months and between seasons, with the lowest records in the wet season.

Sea surface salinity (SSM), varied between 31.60 and 34.90 ppm; it showed its highest densities (>35 ppm) in the wet season from 2016 to 2019, specifically in March, April and May, however, high salinities were also recorded in dry season, particularly in June and July 2018 and August 2019. Likewise, lower salinity densities (<33 ppm) were recorded in dry season, exclusively, in September and November 2016, in November 2017 and 2018 and in August 2018 and 2019, however, salinities lower than <33 ppm were also found in the wet season, specifically in March 2017 and 2018 (Figure 2c). The SSM, during the dry season were mostly concentrated between 33.20 and 33.82 ppm, while in the wet season, between 34.07 ppm to 34.55 ppm (Figure 3e and 3f). Significant differences ($p<0.05$) were detected between months and between seasons, with the lowest records in the wet season.

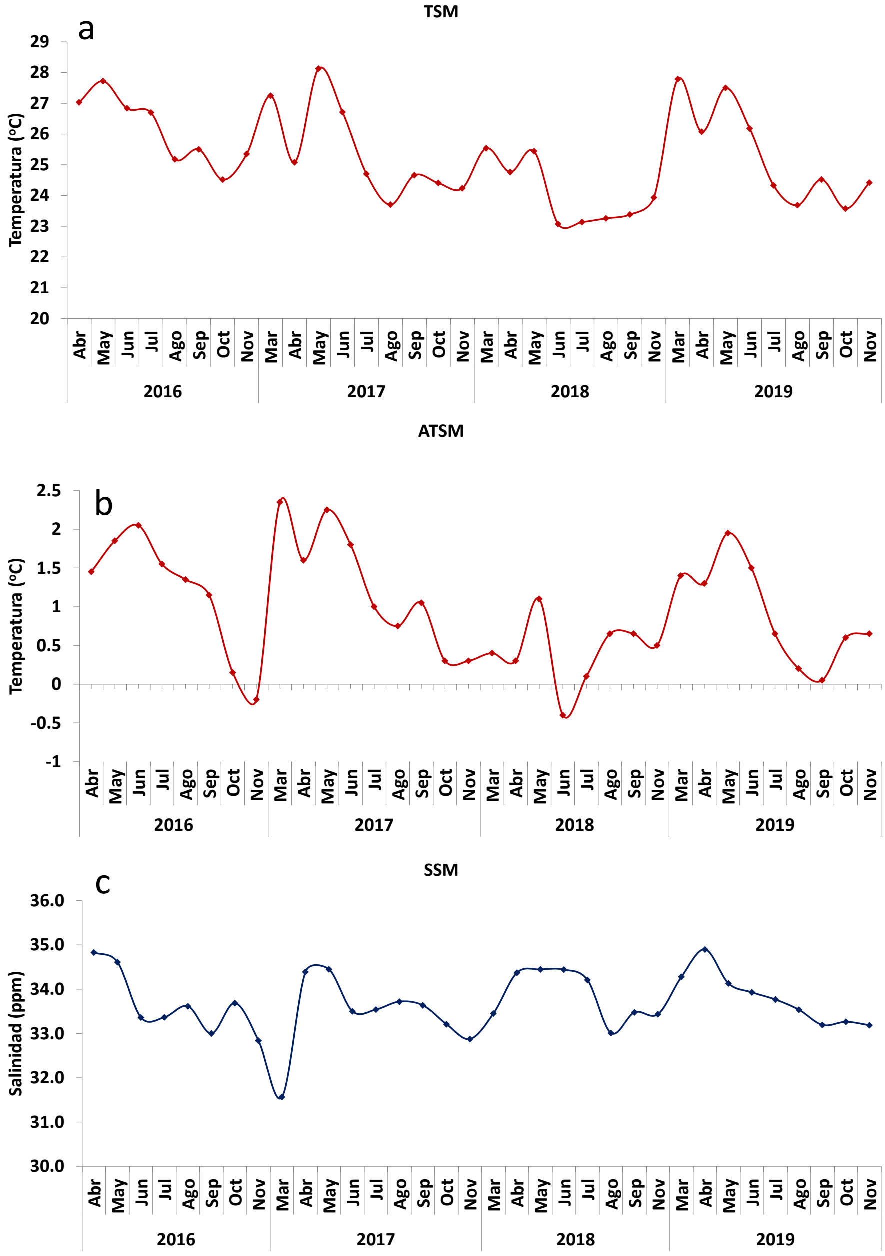


Figure 2*.* SST, ATSM and SSM values during the study period between 2016 and 2019. a=Sea surface temperature; b= Sea surface thermal anomalies; c= Sea surface salinity.

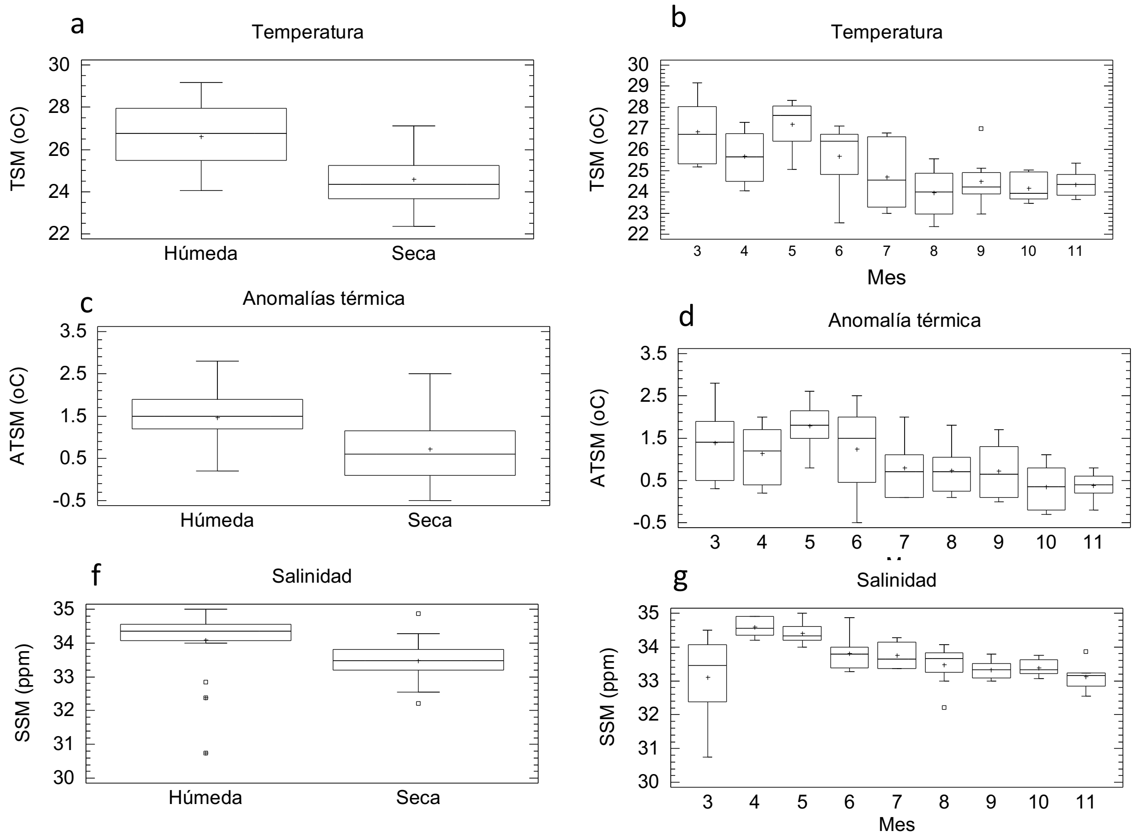
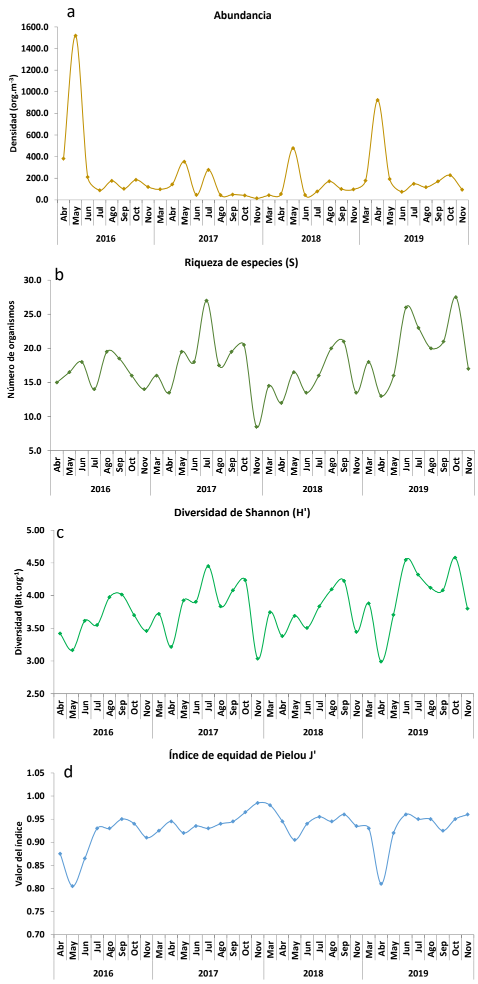


Figure 3. Whisker boxes indicating temperature variations, thermal anomalies and salinity by epoch and monthly in the study area during 2016 to 2019.

Abundance and ecological parameters

From 2016 to 2019, the average abundance of copepods per month, ranged from 14.58 to 1518.53 org.m^{-3} , the minimum density was recorded in November (dry season) of 2017 and the maximum in May (wet season) of 2016 (Figure 4a). Species were more abundant in the wet season, observing a greater range of dispersal, being much more abundant in April and May, most densities were located above 120 org.m^{-3} , while in the dry season, species abundance values were located below 120 org.m^{-3} , with the lowest densities observed in June and September (Figure 5). The average species richness per month, ranged from 8.50 to 27.50 individuals, identifying the minimum value in November 2017 and the maximum in October 2019, dry season months (Figure 4b). The average per month Shannon Diversity Index showed the highest value (4.58 bit.org^{-1}) in October 2019 and the lowest (2.22 bit.org^{-1}) in April 2019; the range of amplitude of the Diversity Index shows that species composition was variable over time revealing a diverse copepod community. The average Simpson's Index per month, presented a range from 0.81 to 0.99, the low value was recorded in May 2016 and the high value in November 2017 (Figure 4d). The Index indicated the degree of dominance of one or two species in the months of April, May and June 2016, in the rest of the months and year, the species distribution was more equal. The values of the index of diversity, species richness and species equity were higher in the dry season, however, the range of dispersion of the variables was similar to those of the wet season.



Temporal distribution of abundance (a), species richness (b), of diversity index (c) and equity index (d) in study area from 2016 to 2019.
a= Abundances; b=Diversity= Shannon-Wiener (H'); c=Species richness=S; c=Margalet index= D_{Mg} : Pielou equity index=J`.

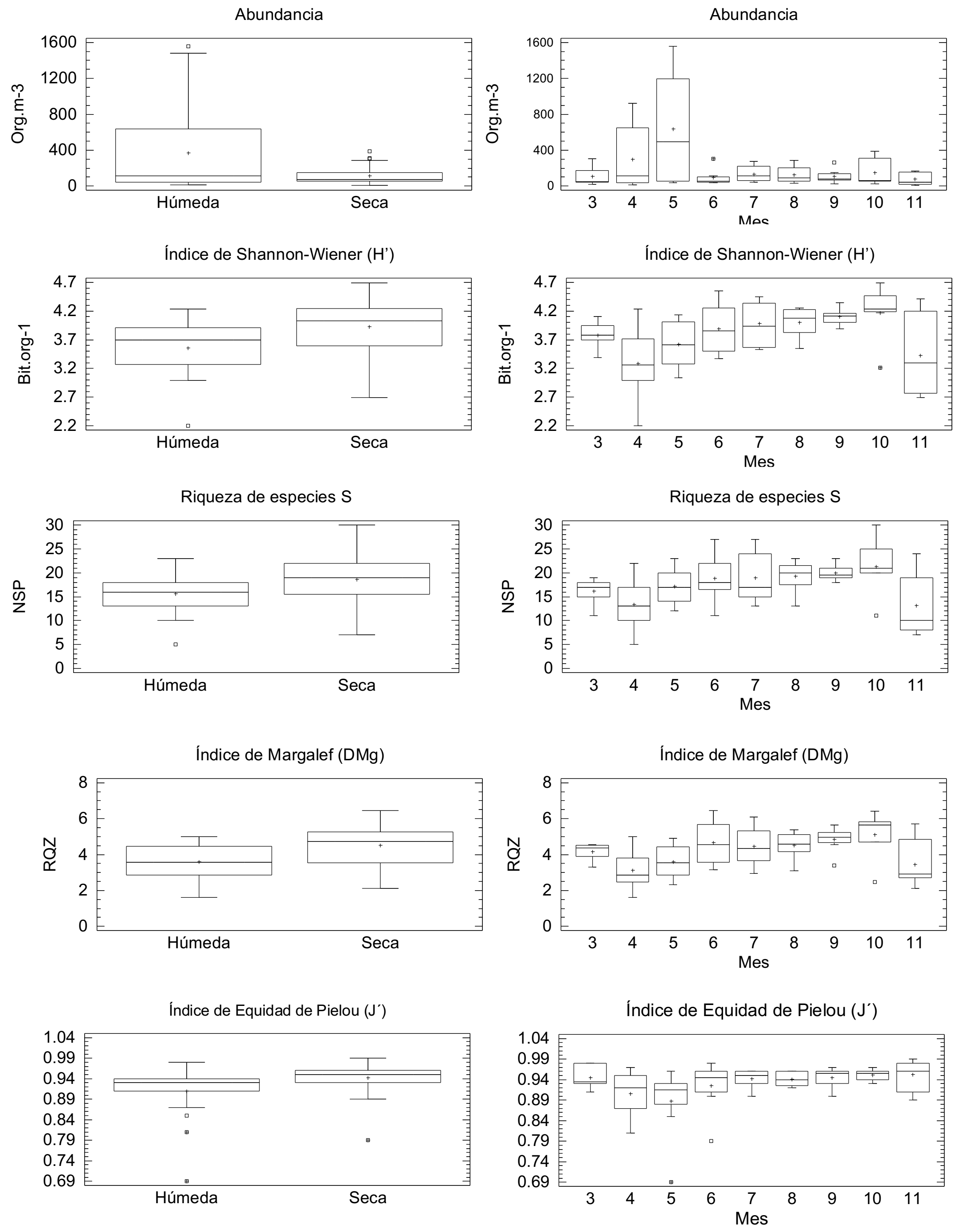


Figure 5. Variation in abundance, diversity, richness and copepod equity by season and monthly in the study area from 2016 to 2019. Diversity= Shannon-Wiener (H'); Species richness=S; Margalet index= D_{Mg} : Pielou equity index=J`.

Copepod community composition

In this study, 68 species of copepods were identified (Table 1), grouped into four orders, of which 43 were Calanoids, 22 were Cyclopoids, 2 were Harpacticoids, and 1 was a Siphonostomatoid. Calanoids constituted 64.18%, Cyclopoids 32.84%, Harpacticoids 2.94%, and Siphonostomatoid 1.47%. A total of 21 780 copepods (juveniles and adults) were found, with species abundance varying between 1 and 2 243 individuals. The copepods, *Canthocalanus pauper*, *Acrocalanus longicornis*, *Oncaea venusta*, *Centropages furcatus*, and *Subeucalanus. pileatus* were the species that recorded total abundance between 998 and 2 243 individuals; *Temora. discaudata*, *A. tonsa*, *Acrocalanus gracilis*, *Corycaeus andrewsi*, *Paracalanus parvus, Clausocalanus furcatus*, *Oithona plumifera, Undinula vulgaris*, *Calolanus pavo*, *Calanopia minor*, *Corycaeus agilis*, *Labidocera acuta*, *Corycaeus amazonicus*, *Pontellina. plumata*, *Corycaeus crassiusculus*, *Subeucalanus crassus* and *Farranula gracilis* recorded a total of between 101 and 774 individuals; the remaining species ranged from 1 to 77 individuals (Table 1).

Table 1. *Copepod species recorded in the study area from 2016 to 2019.*

Nombre científico	Org.m^{-3}	Nombre científico	Org.m^{-3}
Acartia danae (Giesbrecht, 1889)	xx	*Eucalanus sewelli* (Fleminger, 1973)	x
Acartia lilljeborgi (Giesbrecht, 1889)	xx	*Eucalanus subtenuis* (Giesbrecht, 1888)	x
Acartia negligens (Dana, 1849)	xx	*Euchaeta indica* (Wolfenden, 1905)	xx
Acartia tonsa (Dana, 1849)	xxx	*Euchaeta longicornis* (Giesbrecht, 1888)	x
Acrocalanus gracilis (Giesbrecht, 1888)	xxx	*Euchaeta media* (Giesbrecht, 1888)	x
Acrocalanus longicornis (Giesbrecht, 1888)	xxxx	*Farranula gracilis* (Dana, 1849)	xxx
Calanopia mino r (Scott A., 1902)	xxx	*Labidocera acuta* (Dana, 1849)	xxx
Calanus chilensi s (Brodsky, 1959)	xx	*Labidocera detruncata* (Dana, 1849)	x
Caligus rapax Milne (Edwards, 1840)	x	*Lucicutia flavicornis* (Claus, 1863)	x
Calocalanus plumulosus (Claus, 1863) b	x	*Microsetella rosea* (Dana, 1847)	xx
Calocalanus pavo (Dana, 1852)	xxx	*Nannocalanus minor* (Claus, 1863)	xx
Calocalanus pavoninus (Farran, 1936)	xx	*Oithona plumifera* (Baird, 1843)	xxx
Candacia catula simili s (Wolfenden, 1905)	xx	*Oithona rigida* (Giesbrecht, 1896)	xx
Candacia curta (Dana, 1849)	x	*Oithona setigera setigera* (Dana, 1852)	xx
Canthocalanus pauper (Giesbrecht, 1888)	xxxx	*Oncaea cleve* i (Früchtl, 1923)	xx
Centropages bradyi (Wheeler, 1901)	x	*Oncaea conifera* (Giesbrecht, 1891)	x
Centropages furcatus (Dana, 1849)	xxxx	*Oncaea media* (Giesbrecht, 1891)	x
Centropages gracilis (Dana, 1849)	xx	*Oncaea* sp.1	xx
Clausocalanus jobei (Frost & Fleminger, 1968)	xx	*Oncaea venusta* (Philippi, 1843)	xxxx
Clausocalanus furcatus (Brady, 1883)	xxx	*Paracalanus campaneri* (Björnberg T.K.S., 1982)	xxx
Clausocalanus mastigophorus (Claus, 1863)	xx	*Paracalanus parvus* (Claus, 1863)	xxx
Clausocalanus mino r (Sewell, 1929)	x	*Pontellopsis perspicax* (Dana, 1849)	xx
Copilia mirabilis (Dana, 1852)	xx	*Pontellina plumata* (Dana, 1849)	xxx
Corycaeus agilis (Dana, 1849)	xxx	*Pontellopsis lubbockii* (Giesbrecht, 1889)	xx
Corycaeus andrewsi (Farran, 1911)	xxx	*Pseudodiaptomus* sp. (Walter, 1989)	x
Corycaeus crassiusculus (Dana, 1849)	xxx	*Rhincalanus nasutus* (Giesbrecht, 1888)	x
Corycaeus amazonicu s (F.Dahl, 1894)	xxx	*Sapphirina intestinata* (Giesbrecht, 1891)	xx
Corycaeus cf *limbatu*	x	*Sapphirina iris* (Dana, 1849)	x
Corycaeus flaccus (Giesbrecht, 1891)	x	*Sapphirina nigromaculata* (Claus, 1863)	xx
Corycaeus furcife r (Claus, 1863)	x	*Scolecithrix danae* (Lubbock, 1856)	x
Corycaeus ovalis (Claus, 1863)	xxx	*Scolecithricella nicobarica* (Sewell, 1929)	x
Corycaeus speciosus (Dana, 1849)	xx	*Temora discaudata* (Giesbrecht, 1889)	xxx
Eucalanus crassu s (Giesbrecht, 1888)	xxx	*Undinula darwin* i (Lubbock, 1860)	xx
Eucalanus pileatus (Giesbrecht, 1888)	xxxx	*Undinula vulgaris* (Dana, 1849)	xxx

x=	>1	xx=	>10	xxx=	>100	xxxx=	>1000

Spatio-temporal abundance of copepods

In the wet season, 8 892 copepods were found, consisting of 56 species, the most abundant being *Canthocalanus pauper*, *Acrocalanus longicornis, Oncaea venusta* and *Centropages furcatus*, which represented 12.65, 19.31, 12.58 and 10.77%, respectively. In dry season, 6 728 copepods were found, represented by 58 species of which: *C. pauper*, *S. pileatus* and *O. venusta* were more abundant, each contributing 19.07, 9.73 and 7.63 %, respectively. Fifty species were concurrent in both seasons. Eleven species did not participate in the wet season and 10 in the dry season. In Manta, 7 334 copepods composed of 61 species were recorded, the most important being *C. pauper*, *A. longicornis S. pileatus* and *O. venusta*, which each contributed 19.32, 15.59, 7.03 and 6.72 %, respectively. In La Libertad, 8 050 copepods composed of 60 species were recorded, with *O. venusta*, *C. pauper*, *A. longicornis* and *C. furcatus accounting* for 14.15, 11.99, 10.86 and 10.84 %, respectively, and 53 species participated in both stations. Seven specimens were not present in Manta and eight specimens in La Libertad. Table 2 summarizes the presence and absence of species during the study period by time and season.

Table 2. *Uncommon copepod species not during the study period by season and by area from 2016 to 2019.*

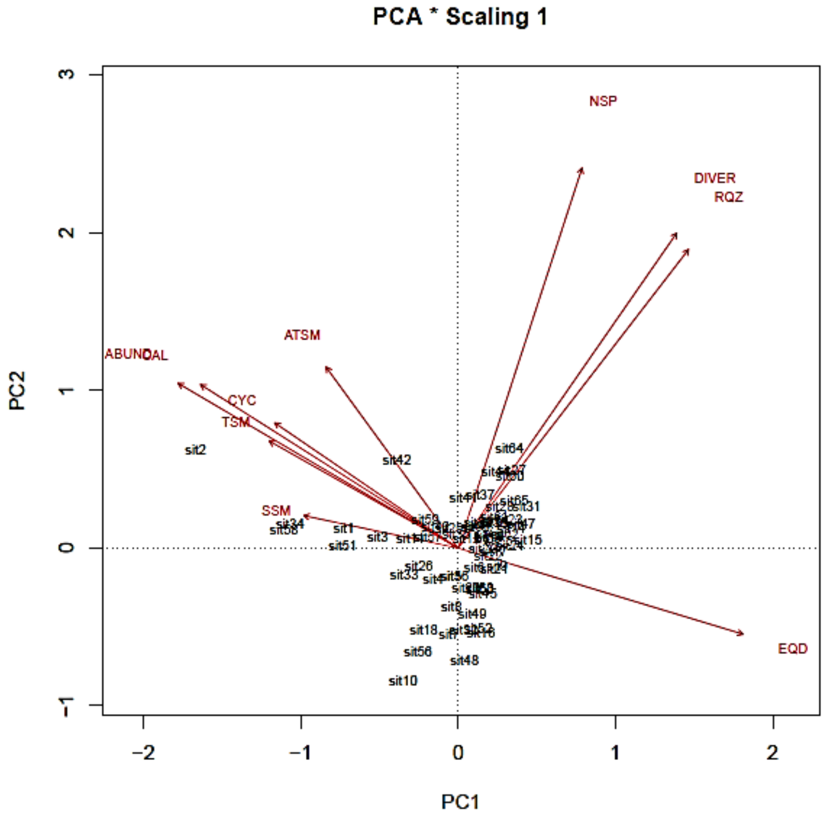
	EPOCA	
Nombre científico	**Humeda**	**Seca**
Acartia danae (Giesbrecht, 1889)	xx	
Acartia negligens (Dana, 1849)		xx
Caligus rapax (Milne Edwards, 1840)		x
Calocalanus plumulosus (Claus, 1863)		x
Candacia catula simili s (Wolfenden, 1905)		xx
Candacia curta (Dana, 1849)	x	
Centropages bradyi (Wheeler, 1901)		x
Clausocalanus mino r (Sewell, 1929)		x
Corycaeus cf *limbatu*	x	
Eucalanus crassu s (Giesbrecht, 1888)		xxx
Eucalanus subtenuis (Giesbrecht, 1888)		x
Euchaeta media (Giesbrecht, 1888)	x	
Microsetella rosea (Dana, 1847)		xx
Oncaea conifera (Giesbrecht, 1891)	x	
Oncaea media (Giesbrecht, 1891)	x	
Oncaea sp.1	xx	
Pontellopsis perspicax (Dana, 1849)	xx	
Pseudodiaptomus sp. (Walter, 1989)		x
Rhincalanus nasutus (Giesbrecht, 1888)	x	
Sapphirina iris (Dana, 1849)	x	
Sapphirina nigromaculata (Claus, 1863)		xx

	ESTACIÓN	
Nombre científico	**Manta**	**La Libertad**
Acartia danae (Giesbrecht, 1889)	xx	
Caligus rapax (Milne Edwards, 1840)	x	
Candacia curta (Dana, 1849)	x	
Centropages bradyi (Wheeler, 1901)		x
Clausocalanus mino r (Sewell, 1929)	x	
Corycaeus cf *limbatu*		x
Eucalanus crassu s (Giesbrecht, 1888)	xxx	
Eucalanus subtenuis (Giesbrecht, 1888)		x
Euchaeta longicornis (Giesbrecht, 1888)		x
Euchaeta media (Giesbrecht, 1888)	x	
Oithona setigera setigera (Dana, 1852)		xx
Oncaea conifera (Giesbrecht, 1891)	x	
Oncaea media (Giesbrecht, 1891)		x
Pseudodiaptomus sp. (Walter, 1989)		x
Rhincalanus nasutus (Giesbrecht, 1888)	x	

x= >1 xx= >10 xxx= >100

Principal Component Analysis

The analysis of the hydrographic and biological variables through the PCA showed 63% of accumulated variance in the first two components; the first axis positively related species equity and negatively related salinity, temperature, abundance, calanoids and cyclopoids. This component measured the behavior of biotic variables as a function of temperature and salinity, since a change in temperature values and salinity concentrations would affect the copepod community, decreasing if salinity increases and vice versa. The second component positively related species richness and diversity and negatively related thermal anomaly. This component would measure the behavior of species richness and diversity as a function of thermal anomaly. Thermal anomaly values would influence species richness and diversity, but a few species would dominate (Figure 4).



Orthogonal projection of the first two components of the Principal Component Analysis (SST: sea surface temperature; SSM: sea surface salinity; ABUND: abundance; NSP: number of species; DIVER: species diversity; RQZ: species richness; EQD: species equity).

Canonical Correspondence Analysis

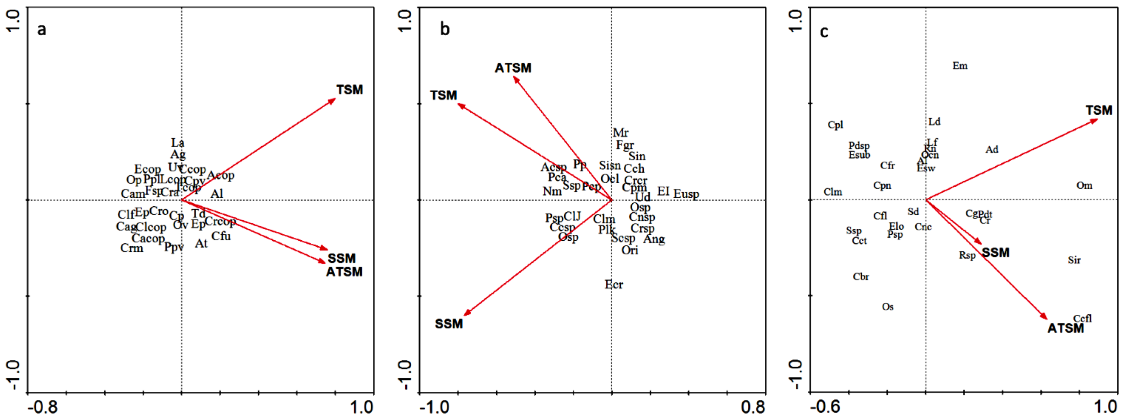
In Figure 7a, the canonical correspondence analysis (CCA) showed that temperature, thermal anomalies and salinity have high correlations with the first axis, so that the positive part of the axis indicates high values of temperature, thermal anomaly and salinity. The analysis allowed the discrimination of four groups around components 1 and 2. The species *Corycaeus* sp, *Acrocalanus* cop, *T. discaudata, S. pileatus*, *Temora* cop, *A. longicornis*, *L. acuta*, *C. pavo*, *Labidocera* cop, *Clausocalanus* cop and *A*. *gracilis* were associated with the positive part of the first axis. Knowing that there is a relationship between the variables and this part of the axis, it can be confirmed that these species were more abundant and frequent when the water bodies registered high values of temperature and salinity. Likewise, the ACC associated the copepods: *Calanus* cop, *Subeucalanus* cop, *C*. *andrewsi*, *C*. *agilis*, *P. parvus*, *Farranula* sp., *Cl. furcatus*, and *S. pileatus*, in the negative part of the axis, this condition indicates that this group of species were abundant and frequent when the water masses registered low values of temperatures and salinity. Similarly, the ACC correlated the species *C. ovalis*, *A .tonsa*, *C .pauper*, P. *plumata*, *Centropages* cop, *C. amazonicus*, C. *minor* and *O. plumifera* to a greater degree with salinity than with temperature. The first four species were positively related and the last four were negatively related, indicating that the first group were abundant in higher salinity water masses and the second group developed in low salinity water masses.

In Figure 7b, the ACC negatively related axis one to temperature and salinity, while axis two was positively associated with the thermal anomaly of the water. The ACC confirmed that the species *Pontellopsis* sp., *C. mastigophorus, Oithona* sp., *Calocalanus* sp., *P. campaneri*, *C. jovei* and *N. minor* were related to elevated values of temperature and salinity, concluding that these species frequented warm water masses with high salinity. Likewise, *U. darwini*, *E. indica, Subeucalanus* sp., *Oncaea* sp., and *Candacia* sp. were related to low temperature and salinity waters. In addition, the ACC related *P. perspicax*, *O. clevei* and *S. intestinata* with high thermal anomalies and contrarily to *M. rosea*, C*. chilensis*, *C. crasiculus*, *P. lubbocki*, *S. crassus* and *O. rigida, S. nigromaculata,* C. *mastigophorus, C. speciosus* and *A. negligens.*

In Figure 7c the ACC shows that temperature and salinity have high correlations with respect to the first axis, while the thermal anomaly has high correlations with each of the two axes. That is, the variable is associated with the positive part of the first axis and with the negative part of the second axis. The species A. *danae*, *S. iris*, *O. media*, *C.* cf *limbatu*, *L. detruncata*, *E. media*, C. *rapax*, *S. subtenuis*, *Scolecitrella* sp, *C. minor*, *O. setigera*, *Pontellina* sp. and *C. catula* were associated with temperature, the first eight with high SST values and the remaining eight with low values. Likewise, *C. flaccus*, *S. iris*, *C. curta*, *C. plumulosus*, *E. media*, *A. lilljeborgi*, *C. pavoninus*, *L. detruncata*, *Scolecitrella sp*, *C. bradyi* were associated with salinity. The first two species frequented high salinities and the rest frequented low salinity waters. Likewise, the ACC associated the species, *C. gracilis*, *Rhincalanus* sp., *S. longicornis*, *L. flavicornis*, *S. danae*, *C. furciter*, *R. nasutus*, *O. conifera*, *Pseudiaptomus* sp., and *S. sewelli* with ATSM. The first five occurred when the thermal anomaly was high and the rest when the anomalies were low.

Table 3 lists the main copepod species with their respective codes to understand ACC graph 7.

Table 4 shows the main species of copepods that are associated with the water masses of the Ecuadorian Pacific, and according to their frequency of occurrence and abundance, the ACC correlated them with temperature and salinity.



Canonical Correspondence Analysis (CCA) ordination plot for species composition and environmental variables (SST, temperature; TSA, thermal anomaly; and SSS, salinity).

Table 3 *shows the species with their respective codes used in Figure 7.*

Figura a		Figura b		Figura c	
Especie	**codigo**	**Especie**	**codigo**	**Especie**	**codigo**
C.pauper	Cp	*C.crassiusculus*	Crcr	*Acartia sp.*	Acsp
A.longicornis	Al	*E.crassus*	Ecr	*A.negligens*	Ang
Acrocalanus sp.	Acop	*F.gracilis*	Fgr	*C.chilensis*	Cch
O.venusta	Ov	*P.campaneri*	Pca	*Calocalanus sp.*	Ccsp
Eucalanus sp.	Ecop	*Sapphirina sp.*	Ssp	*Cl.jovei*	ClJ
C.furcatus	Cfu	*C.speciosus*	Crsp	*Cl.mastigophorus*	Clm
Labidocera sp.	Lcop	*O.clevei*	Ocl	*Candacia sp.*	Cnsp
E.pileatus	Ep	*Cl.mastigophorus*	Clm	*C.mirabilis*	Cpm
C.ovalis	Cro	*Paracalanus sp.*	Pcp	*C.crassiusculus*	Crcr
Temora sp.	Tcop	*Candacia sp.*	Cnsp	*C.speciosus*	Crsp
T.discaudata	Td	*C.mirabilis*	Cpm	*E.crassus*	Ecr
Calanus sp.	Cacop	*Oithona sp.*	Osp	*Eu.indica*	EI
A.tonsa	At	*Eu.indica*	EI	*Eucalanus sp.*	Eusp
A.gracilis	Ag	*Acartia sp.*	Acsp	*F.gracilis*	Fgr
C.andrewsi	Cra	*N.minor*	Nm	*M.rosea*	Mr
P.parvus	Ppv	*Cl.jovei*	ClJ	*N.minor*	Nm
Cl.furcatus	Clf	*Scolecithrix sp.*	Scsp	*O.clevei*	Ocl
O.plumifera	Op	*Oncaea sp.*	Osp	*O.rigida*	Ori
Corycaeus sp.	Crcop	*S.instestinata*	Sin	*Oithona sp.*	Osp
U.vulgaris	Uv	*S.nigromaculata*	Sin	*Oncaea sp.*	Osp
Clausocalanus sp.	Clcop	*P.lubbocki*	Plk	*P.campaneri*	Pca
Farranula sp.	Fsp	*Eucalanus sp.*	Eusp	*Paracalanus sp.*	Pcp
C.pavo	Cpv	*Calocalanus sp.*	Ccsp	*P.lubbocki*	Plk
C.minor	Crm	*O.rigida*	Ori	*P.perspicax*	Pp
C.agilis	Cag	*Pontellopsis sp.*	Psp	*Pontellopsis sp.*	Psp
Euchaeta sp.	Ep	*A.negligens*	Ang	*Scolecithrix sp.*	Scsp
L.acuta	La	*C.chilensis*	Cch	*S.instestinata*	Sin
Centropages sp.	Ccop	*U.darwini*	Ud	*S.nigromaculata*	Sin
C.amazonicus	Cam	*P.perspicax*	Pp	*Sapphirina sp.*	Ssp
P.plumata	Ppl	*M.rosea*	Mr	*U.darwini*	Ud

Table 4. *Copepod species that would be related to water masses in the Ecuadorian Pacific during the study period from 2016 to 2019.*

AguasTropicales Superficiales (ATS)	**Aguas Ecuatoriales Superficiales (AES)**
Acartia negligens (Dana, 1849)	*Corycaeus andrewsi* (Farran, 1911)
Acrocalanus gracilis (Giesbrecht, 1888)	*Calanus chilensis* (Brodsky, 1959)
Acrocalanus longicornis (Giesbrecht, 1888)	*Canthocalanus pauper* (Giesbrecht, 1888)
Calocalanus pavo (Dana, 1852)	*Clausocalanus furcatus* (Brady, 1883)
Centropages furcatus (Dana, 1849)	*Corycaeus agilis* (Dana, 1849)
Corycaeus speciosus (Dana, 1849)	*Corycaeus ovalis (Claus, 1863)*
*Euchaeta indica (*Wolfenden,1905)	*Oithona rigida (Giesbrecht, 1896)*
Labidocera acuta (Dana, 1849)	*Paracalanus parvus* (Claus, 1863)
Temora discaudata (Giesbrecht, 1889)	*Subeucalanus pileatus* (Giesbrecht, 1888)

Discussion

The planktonic copepod community investigated in this study showed that it occupies a key position in the ecosystems of Manta and La Libertad, being the main secondary producers in the study area, since they formed a community that reached 68 species, constituting a large part of the zooplankton biomass. Studies conducted in the Ecuadorian Pacific, show that copepods constitute approximately 80% of the total zooplankton (Prado and Cajas. 2009; Coello et *al.* 2010 and Cajas. 2017). Likewise, studies conducted in other areas of the ocean indicate that copepods contribute a high percentage to the total zooplankton (Drira *et al*. 2010; Fernández *et al.* 2019). It is possible that the copepods in this study could also have contributed to the zooplankton biomass in that percentage. This research contributes to evidence that copepods are the main component of zooplankton in the Ecuadorian Pacific.

During the study, spatiotemporal variations in temperature, thermal anomalies and salinity at the sea surface caused changes in abundance, diversity and species richness (Figure 2). This is because the different physical and chemical parameters impact the development and abundance of zooplankton (Diaz-Zabella & Gaudy. 1996; Suresh *et al.* 2011), since marine systems are very dynamic and cause these changes on daily, seasonal and interdecadal time scales (Record, *et al.* 2010). Then the analysis of the effect of hydrological changes on the planktonic community provides insight into the effects of short- and long-term climate variability on copepod community structure, such as those driven by ENSO (Piontkovski & Landry, 2003; Jiménez-Pérez, 2016; Kozak *et al.* 2018).

During December 2016 to May 2017, the "coastal El Niño" was activated. In that period, sea surface temperature increased abruptly, reaching values above 26°C on the southern coast of Ecuador (La Libertad) and northern Peru, when in the central equatorial Pacific the La Niña phenomenon was still occurring (ENFEN. 2017;

Takahashi, 2017). However, the increase in temperature in the study area did not lead to an increase in copepod densities, but species associated with warm water masses such as *A. longicornis*, *C. pauper*, *C. ovalis*, *S. pileatus* dominated (Boltovskoy. 1981; Boltovskoy. 1999); which would suggest that the event did not have a major influence on the fixed stations 10 miles off Ecuador.

On the other hand, during the study, the month of May of each year, the highest values of temperature, salinity and abundance of copepods were recorded, but low values of diversity and species richness. This characteristic would be related to the transition from the wet season to the dry season, since May is considered a transition month (Cucalón, 1989). And it is when the position of the equatorial front would be at the height of the Gulf of Guayaquil (ERFEN, 2016), fertilizing the coastal waters of the study area (Trejos, et al. 1983). This oceanographic condition would be the cause of the characteristics observed in the month of May of each year of study.

So far, the maximum number of copepods recorded in the Ecuadorian Pacific was reported by Tutasi *et al.* (2011), with 104 species. This was followed by the study conducted by Martínez. (2019) who recorded 95 species and by Bucheli and Cajas (2020) who identified 63 species of copepods. In this research, 68 species were reported. The difference is due to the type of sampling applied. Thus, Tutasi *et al*. (2011), performed oblique trawling from 150 m to 0 m and Martinez. (2019), vertical trawling from 50 m to 0 m and Bucheli and Cajas (2020) applied surface trawling. In this research, surface trawling was applied, but in two stations, which explains the difference in species richness.

In comparison with other areas of the eastern Pacific, Hernández *et al.* (2004) recorded 152 copepod species in Bahía Magdalena, Baja California Sur, Mexico. Jerez *et al.* (2017) identified 54 copepod species in Bahía Cupica the Colombian Pacific. In both studies, calanoid copepods were the most abundant and diverse, equal to this study.

In the study presented here, distinct copepod clustering trends were observed as a function of a given environmental parameter. The species: *C. pauper*, *A. longicornis*, *O. venusta*, *C. furcatus*, *S. pileatus*, *C. ovalis*, *T. discaudata*, *A. tonsa*, A. *gracilis*, *D. andrewsi*, *P. parvus Cl. furcatus* and *O. plumifera*, were permanent residents of the study area. While: *R. nasutus*, *O.conifera*, *Pseudiaptomus* sp., *O. media*, C. *bradyi*, *C.rapax*, *P. destruncata*, *S. subtenuis* and *Corycaeus* cf *limbatu* occurred occasionally in the study area. This is explained because the species of the first group could have high degree of tolerance to environmental changes managing to withstand wide temperature and salinity intervals, while the second group tolerance range may be narrower, similar observation reported Lenz. (2012) and Brun *et al*. (2016). Coincidentally, Prado and Cajas (2009), Coello et al. (2010) and Cajas (2017), reported the vast majority of these species as the most concurrent in other areas of the Ecuadorian coast. However, species varied in abundance and dominant species succession when

SST, ATSM AND SSM varied in their magnitudes.

The copepod species identified during the study period are from epipelagic environments associated with tropical and subtropical waters (Monsalve, 1976; Palomares et al., 1998; Boltovskoy, 1985 and Boltovskoy, 1999; Razouls *et al*., 2017). The greatest number of these species are distributed along the Eastern Pacific (Arcos and Fleminger 1986; Ayón et al. 2008; Tutasi et al. 2011; López & Mojica. 2015; Mojica and Herrera. 2019; Jerez et al. 2017).

In this study, the copepod community was most abundant during winter conditions with densities reaching between 500 and 1500 org.m^{-3} . Prado and Cajas (2009) observed the same pattern in the Esmeraldas area, but with total zooplankton, where copepods were the most abundant group. However, this was not the case in the area of Punta Galera and Puerto López, where the highest abundance was recorded in April and December, respectively. Something similar occurred with what was observed by Coello *et al* (2010) in the area of Puerto López.

The highest diversity and richness observed in July and October differs from that reported by Prado and Cajas (2009), who recorded the highest diversity values in September. However, both studies coincide with the highest diversity in the dry season. Studies on copepod diversity by Siokou-Frangou *et al.* (1996), Daly Yahia *et al*. (2004) and Ben et al. (2015) in the Mediterranean Sea, observed higher copepod diversity in the winter season, in contrast to what was observed in this study.

It is important to keep in mind that there are few studies on diversity and richness of copepods in the Ecuadorian Pacific, and the few studies have been conducted in stations 10 miles from the coast, so it cannot be said that the diversity and richness of copepods is greater in the dry season. For this, more studies need to be carried out in various points of the Ecuadorian sea. However, the Shannon index revealed a variable diversity over time where a single or few species often numerically control the community.

On the other hand, the PCA results showed that the abundance of calanoids and cyclopoids was strongly influenced by high temperature and low salinity values. But species richness and diversity were affected by negative thermal anomalies. These relationships suggest that calanoids and cyclopoids associated with warm water masses increased their abundances with low dominance of a few species, causing species richness and diversity indices to be low. On the other hand, when the water masses were colder and more saline, the species would be homogeneously distributed, causing the value of the richness and diversity indices to be high. These characteristics are evident in the wet and dry season. Overall, these PCA correlations show that variations in temperature and salinity reflect changes in the different water masses that shape copepod abundance, composition, and diversity, similar to what was observed by Medellin et al. (2021). Then, from principal component analyses, it was understood that copepod abundance, richness and diversity were significantly different from one season to another and, mainly, copepod structure and dynamics in the Ecuadorian Pacific were structured by seasonal water mass patterns.

Similar to the PCA, the canonical correspondence analysis evidenced that the measured abiotic factors (temperature and salinity) influenced to a greater or lesser extent the frequency of occurrence of copepod species during the study period, similar to what was observed by Ben *et al.* (2015) in the Gulf of Tunisia (southwestern Mediterranean Sea). For example, species that were positively associated with high temperature and low salinity clearly indicated the affinity these copepods for tropical water masses (ATS), while species that correlated negatively with low temperature and high salinity indicates the affinity of these species to equatorial water mass (AES) (Okuda, et al.1983; Valencia. 1996; Zuta and Guillén.1970), water masses that would intensify according to the time. It was understood that the frequency of occurrence of copepod species was significantly different from one seasonal period to another, since the dynamics of the species in the Ecuadorian Pacific were structured by seasonal water mass patterns.

Conclusion

The surface waters of the study area, the temporal and spatial variation of temperature and salinity of the sea influenced the variations in abundance, diversity and richness of copepod species in a special and temporal manner. The highest diversities and richness were evident in the dry season and the lowest in the wet season. This was evidenced by the results of the correlations of the PCA and CCA analyses. In addition, the multivariate analysis determined groups of species that could be associated with Tropical Surface Waters (mainly *A. longicornis*, A. *gracilis and T. discaudata*) and species to Equatorial Surface Waters (mainly *C. furcatus*, *U. darwini* and *E. longicornis*). The results of the research established that the structure and dynamics of copepods in the Ecuadorian Pacific were structured by seasonal water mass patterns.

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