Nauplius
The Journal of The Brazilian Crustacean Society

e-ISSN 2358-2936
www.scielo.br/nau
www.crustacea.org.br

Original Article

Latitudinal and seasonal variation in the copepods (Multicrustacea: Copepoda) of the Gulf of California based on the CORTES cruises (1985)

Karl Edward Velázquez-Ornelas[1]
Michel E. Hendrickx[2]

1 Posgrado en Ciencias del Mar y Limnología, Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Av. Universidad 3000, Ciudad Universitaria Coyoacán, Ciudad de México, México.
KVO kevelazquez@hotmail.com

2 Laboratorio de Invertebrados Bentónicos, Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Av. Joel Montes Camarena S/N, Mazatlán, Sinaloa, México.
MEH michel@ola.icmyl.unam.mx

ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub:522C967D-779F-411B-BA51-28DBA316BC61

ABSTRACT

The Gulf of California is known for its high productivity, diversity, and unique oceanography. Based on old and recent contributions, we estimate a richness of 160 copepod species in this province. This work seeks to identify latitudinal and seasonal patterns of the copepod composition, abundance, and diversity in the Gulf of California during 1985. Differences between four zones of the gulf (NGC, CGC, SGC, EGC) and between the cold and warm seasons were hypothesized, based on taxonomic and ecological data. Samples were collected during the CORTES cruises (1985), which also measured salinity, temperature, and dissolved oxygen at each station. We analyzed the latitudinal and seasonal variation of the copepod community with multivariate analyses (NMDS-PCA) and correlated these with the environmental data (CCA). Seventy-nine copepod species were identified, averaging 265,649 and 98,885 ind/10 m^3 in the cold and warm seasons, respectively. Only 53 of these occurred in both seasons, indicating seasonal change in species composition. Composition and diversity varied latitudinally in the cold season ($P < 0.05$ in all comparisons but CGC vs. SGC), but not in the warm season (except NGC vs. the rest of the gulf). There was seasonal change in the composition and the abundance ($P < 0.005$ cold vs. warm season). Richness and diversity were negatively correlated with salinity (decreasing from the north of the gulf); the abundance and composition were mainly affected by the shift in temperature. These patterns also match the phytoplankton abundance and size structure in the gulf, probably the main factors affecting copepod distribution.

Corresponding Author
Karl Edward Velázquez-Ornelas
kevelazquez@hotmail.com

Submitted 28 January 2023
Accepted 26 July 2023
Published 04 December 2023

DOI 10.1590/2358-2936e2023027

KEYWORDS

Early oceanography, El Niño, epipelagic zooplankton, marine diversity, multivariate analysis, taxonomic composition, zooplankton abundance

INTRODUCTION

The Gulf of California is the only enclosed sea of the eastern subtropical Pacific and the only large evaporation basin in the Pacific Ocean, subjected to an intense mixing process near the coast due to the action of the daily tides (Argote et al., 1995; Lavín et al., 1997; Castro et al., 2000). The biological diversity of this sea has been widely studied because of its high level of endemism and particular oceanographic conditions (Hendrickx et al., 2007; Hastings et al., 2010; Angulo-Campillo et al., 2011; Lavaniegos et al., 2012; González-Acosta et al., 2021). The tropical-subtropical Gulf of California is known for its moderate to high biological productivity, comparable to what has been reported in large upwelling zones, like the Bay of Bengal in the Indian Ocean or the west coast of the Baja California Peninsula (Zeitzschel, 1969; Brusca et al., 2005). It is also the habitat of very diverse and abundant invertebrate and vertebrate communities supporting some of the most important fisheries in Mexico (Brusca et al., 2005; Páez-Osuna et al., 2017; Munguia et al., 2018).

The class Copepoda is one of the major groups of the zooplankton, both in abundance and richness. This group of crustaceans currently includes about 14,000 valid species, more than 80% occurring in the marine environment (Suárez-Morales et al., 2020; Walter and Boxshall, 2023). More than 200 pelagic copepod species have been recorded in the Eastern Tropical Pacific (Chen, 1986; Suárez-Morales and Gasca, 1998; Palomares-García et al., 2018; Razouls et al., 2023). We estimate the pelagic copepod richness for the Gulf of California to be close to 160 species, based on old and recent contributions (Jiménez-Pérez and Lara Lara, 1988; Lavaniegos-Espejo and Lara-Lara, 1990; Palomares-García et al., 1998; Suárez-Morales and Gasca, 1998; Palomares-García et al., 2013; 2018; Gómez-Gutiérrez et al., 2014; Álvarez-Tello et al., 2015; Jiménez-Pérez, 2016; Cruz-Hernández et al., 2018; Palomares-García et al., 2018; Beltrán-Castro et al., 2020).

The copepod community of the Gulf of California has been studied under different approaches. For example, Palomares-García et al. (2013) and Cruz-Hernández et al. (2018; 2019) studied the composition and vertical abundance of copepods and their relation to environmental variables. Other studies have described the species composition in selected areas (e.g., Fleminger, 1975; Suárez-Morales and Gasca, 1998; Palomares-García et al., 2018). Some contributions have focused on copepod species endemic to the Gulf of California (e.g., Wolfenden, 1905; Fleminger, 1983; Humes, 1987). Based on all these publications we can conclude that there are only a few (around 10) species which comprise up to 85% of the entire copepod fauna, that most of the abundance remains in the first 75 m of the water column and that the expected richness during a single annual cycle should be around 50–60 species.

The copepod abundance and community composition in the Gulf of California is known to vary along seasonal (e.g., Palomares-García et al., 2013) and interannual (e.g., Beltrán-Castro et al., 2020) cycles, which limits the value of short-term studies in small areas. Ideally, it is therefore desirable to analyze the structure of the copepod communities over several years in large areas in order to maximize our knowledge of this group's distribution and its relationship to oceanographic conditions. However, in many cases the cost of long-term sampling operations and analyses of a large amount of samples is highly expensive. Therefore, it is relevant to take advantage of available historical sample collections to provide baseline information to compare with further oceanographic cruises. The large series of samples collected in the Gulf of California during the cold and warm seasons in 1985 allows for analysis of the copepod community in early Mexican oceanography with the initiation of the R/V "El Puma" in 1980. These samples have been previously used to study the distribution and abundance of *Lucifer typus* H. Milne Edwards, 1837 (Hendrickx and Estrada-Navarrete, 1994), of phylosoma larvae of spiny lobsters (García-Rodríguez et al., 2008) and of Brachyura (see Hendrickx, 1987).

An oceanographic approach to conditions in the Gulf of California can help to better understand how and why the copepod community varies in this area. The Gulf of California is about 283,000 km^2 with depths of up to 3,500 m at the mouth (Hamilton, 1961). According to Brusca et al. (2005) and Hendrickx et al. (2007) it extends from the Colorado River Delta in the north to a line between San Lucas Cape (Baja California Sur) and Corrientes Cape (Jalisco) in the south. The gulf presents increasing depth from the northernmost zone to the entrance; the north zone is particularly shallow, with an average depth of less than 200 m (Lavín and Marinone, 2003). The north zone of the gulf is also characterized by saltier waters due to long residence times (Lavín et al., 1995) caused by a circulation pattern dominated by an anticyclonic gyre (Lavín et al., 2014); and it presents a wide variation in water parameters because of its shallow depth (Álvarez-Borrego and Galindo, 1974). The Gulf of California is known for its seasonally reversing winds (Wyrtki, 1965; Brinton and Towsend, 1980), which change the upwelling line position from the east coast during winter to the west coast during summer and cause a seasonally reversing flow pattern in the surface waters (Badan-Dangon et al., 1985; Álvarez-Borrego and Lara-Lara, 1991; Lavín et al., 2014). There is also a seasonal pattern for the latitudinal movement of the water masses: the waters from the Eastern Tropical Pacific and the subtropical subsurface waters enter only at the mouth of the gulf during winter, while these invade the whole gulf during summer (Álvarez-Borrego and Schwartzlose, 1979). The waters of the Gulf of California are usually warmer compared to other water masses in similar latitudes; and this Gulf of California Water (GCW) has a salinity of ≥ 35 in the upper layers (Castro et al., 2000; Lavin and Marinone, 2003; Álvarez-Borrego and Lara-Lara, 1991). The temperature flux has been observed to increase from the entrance to the north, gaining heat along its overall length with a maximum flux in June and mainly along the east coast closest to the Tropical Surface Water (TSW) (Portela et al., 2016). Salinity doesn't show a clear seasonal pattern (Castro et al., 1994), but due to the entrance of the previously mentioned water masses it varies widely latitudinally. The interannual variability is related to atmospheric changes, associated with El Niño-Southern Oscillation (ENSO) events (Durazo et al., 2005). The 1982–1983 El Niño was one of the strongest recorded for this province, bringing fresher and warmer waters of tropical origin into the entrance of the gulf (Lavín et al., 2003). ENSO episodes tend to coincide with low productivity, due to the increase in surface temperatures above 28 °C (Santamaría-del-Angel et al., 1994), although Valdéz-Holguín and Lara-Lara (1987) reported higher productivity during the 1982–1983 ENSO event. In 1985 the oceanographic conditions were influenced by a weak La Niña event (Storlazzi and Griggs, 1998), which diminished the surface temperature of the Gulf of California waters below the average from January to June (NOAA, 2023). The primary productivity in the Gulf of California during 1985 was, according to Lara-Lara et al. (1993), returning to normal levels after the 1982 ENSO.

This study seeks to answer three main questions: 1. What was the epipelagic copepod community composition in the Gulf of California during March and July–August 1985 and how does it compare to other years? 2. What was the spatial and temporal variation of the composition, diversity and abundance of these copepods in 1985? 3. How do environmental variables (salinity, temperature and dissolved oxygen concentration) recorded during the cold and warm periods of this year influence the distribution patterns of abundance, composition, and diversity of the copepod community in the Gulf of California? In order to answer these questions about the distribution patterns of the copepods in the Gulf of California we have hypothesized that there are significant differences in the composition, abundance, and diversity of the copepods among the four defined zones of the Gulf of California and between the two seasons of 1985, caused by latitudinal and seasonal variation in the water masses of the gulf.

MATERIAL AND METHODS

Fieldwork

In order to perform a spatial analysis of the copepod communities in the Gulf of California, we have considered four different zones based on several criteria, including bathymetry (Merrifield and Winant, 1989), hydrography (Álvarez-Borrego, 1983; Álvarez-Borrego and Lara-Lara, 1991), and biogeographic distribution of different groups, including benthic species (Brinton and Towsend, 1980; Brinton et al., 1986; Brusca et al., 2005; Hendrickx et al., 2007; Ulate et al., 2016) or phytoplankton (in terms of taxonomy and abundance) (Gilbert and Allen, 1943; Santamaria-del-Angel and Alvarez-Borrego, 1994; Mercado-Santana et al., 2017; Robles-Tamayo et al., 2020).

The gulf was divided into four zones according to these works: the Northern Gulf of California (NGC), which extends from the Colorado River Delta to a line between San Francisquito Bay, Baja California and Kino Bay, Sonora; the Central Gulf of California (CGC), limited by a line extending between Bahía Agua Verde, Baja California Sur and Bahía de Agiabampo, Sinaloa; the Southern Gulf of California (SGC), extending from the limits marked by Cabo San Lucas, Baja California Sur and Ponce, Sinaloa and, finally, the entrance of the Gulf of California (EGC), which extends up to the limits of the Gulf, marked by Cabo San Lucas, Baja California Sur and Cabo Corrientes, Jalisco (Fig. 1).

The oceanographic cruises CORTES 2, referred herein as the "cold season" (March 1985), and CORTES 3, the "warm season" (July–August 1985), covered the entire Gulf of California with almost the same sampling stations. The sampling grid included 63 stations in each cruise and zooplankton samples were collected in 21 stations of this grid (Fig. 1). For each zooplankton tow, a non-closing Bongo structure with a mouth diameter of 60 cm equipped with two 333/505 µm mesh size nets was deployed. Oblique tows went from a maximum depth of 220 m to the surface, and the sampled volume of water ranged from 98 to 432 m^3. Samples were fixed with a 4% formaldehyde solution, later washed with tap water and then preserved in 70% ethanol. Salinity, temperature and dissolved oxygen concentration were measured at the 63 stations and at three levels of depth: 5 m, 20 m and 75 m. Water was collected with Niskin bottles to measure salinity (conductivity meter) and dissolved oxygen (Winkler method). Temperature was measured in situ with reversing thermometers.

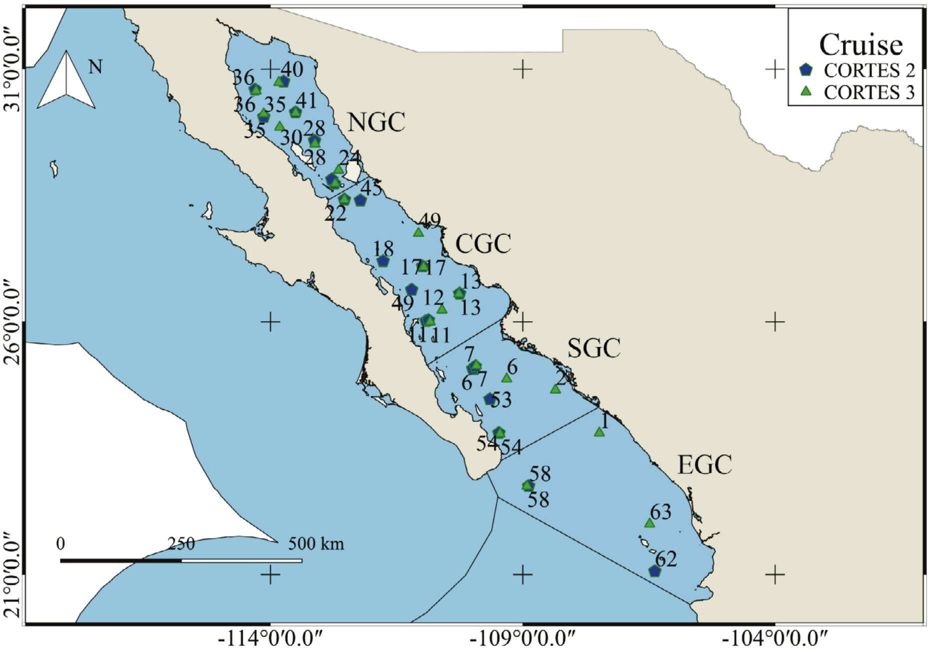

Figure 1. Zooplankton sampling stations in the Gulf of California during the CORTES cruises, in 1985. The four zones of the gulf are, as following: NGC, Northern Gulf of California, CGC, Central Gulf of California, SGC, Southern Gulf of California, and EGC, Entrance of the Gulf of California.

A General Oceanics® flow meter was used to estimate the distance (d) covered by the net. Filtered volume was obtained by using standard methods (Smith and Richardson, 1977). Densities of copepods are herein expressed as the number of organisms in 1,000 cubic meters (ind/10 m^3).

Taxonomic and ecological data collection

Species were identified based on the morphological characters of each morphospecies and based mainly on the work of Palomares-García et al. (1998). When needed, specimens were dissected in order to reduce the taxonomic uncertainty to a minimum. The number of specimens of each species per sample was estimated by counting individuals in the entire sample or in fraction aliquots (Folsom splitter/Stempel pipette), depending upon the abundance of specimens in each sample (1/2 – 1/8 of the original sample). Counting of specimens in samples or subsamples was performed using a Bogorov chamber.

Data analysis

The spatial (i.e., NGC, CGC, SGC and EGC) and temporal (i.e., cold and warm season) variation of the copepod composition was analyzed with a Non-metric Multidimensional Scaling analysis (NMDS) for each cruise (and combined), with previous square root transformation of the data to reduce the distance between samples. Vectors for the species were added to illustrate the Pearson correlation of their abundance in relation to the sampling stations. A SIMPER analysis was performed to identify the species with the highest contribution to the dissimilitude between the two seasons and between the four zones. NMDS and SIMPER analyses were performed in the PRIMER-e 6.0 software. The spatial and temporal variation patterns for abundance, richness and diversity (Shannon-Wiener diversity index) were analyzed with a Principal Component Analysis (PCA) for each cruise (and combined), with previous normalization of the data in PRIMER-e 6.0. We tested the significance of the differences in composition and diversity between the two seasons and between the four zones with permutational MANOVAs, using independent one-factor tests for the spatial variation (Zones) and also for the seasonal variation (Cruises) in the PRIMER-e 6.0 program.

The environmental data was plotted on maps in order to analyze its latitudinal variation, while boxplot graphics were used to analyze its vertical variation. Maps were done using the QGIS 3.14.0 program, and boxplot graphics (95% confidence interval) were done in SigmaPlot 11.0. To correlate the environmental variation with the biological variables (composition, abundance and diversity), we performed a Canonical Correlation Analysis (CCA) for each depth level, with previous normalization of the environmental data and square root transformation of the biological data in the Canoco 4.5 software. The significance of the first four axes was tested with Monte-Carlo permutation tests in the same program.

RESULTS

Composition and abundance

Abundance estimations were significantly different for each season. For the cold season, the average value for the abundance was of 265,649 ind/10 m^3, with a lowest density of 26,395 ind/10 m^3 and a highest of 1,021,076 ind/10 m^3. For the warm season, the average observed abundance was much lower (98,885 ind/10 m^3), with low and high densities of 7,748 and 388,715 ind/10 m^3, respectively. In total, 79 species were recorded: 64 collected in the cold season and 66 in the warm season (Appendix - Tab. A1). For both seasons, the most diverse order was clearly Calanoida (cold season, 45 species; warm season, 48 species), followed by Cyclopoida (cold season, 16 species; warm season, 14 species), and Harpacticoida (cold season, 3 species; warm season, 2 species). Rarefaction curves provided an estimation of nearly 90 species expected for the highest estimations (Jackknife 1 and 2); Jackknife 2 and Chao 2 estimators reached the asymptote (Fig. 2). Overall, the richness observed in the cold and warm seasons was very similar, with only 26 species not shared between the two cruises. The lowest shared richness was observed for the family Pontellidae: 4 species in the cold season vs. 10 in the warm season (Appendix – Tab. A1). Pontellids were also much less abundant in the cold season (0.72% of the abundance) than in the warm season (3.45%); *Labidocera jollae* appeared uniquely in the cold season. The rest of the families maintained a similar richness between both seasons (Appendix – Tab. A1).

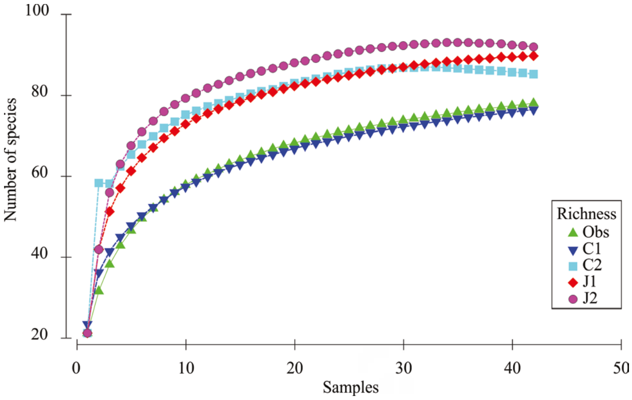

Figure 2. Estimation of the expected copepod richness for the Gulf of California in 1985. Rarefaction curves are based on the sampled stations of the CORTES 2 and 3 cruises. Curves correspond to the observed number of species (Obs) and to the non-parametrical indicators: Chao 1 (C1), Chao 2 (C2), Jackknife 1 (J1) and Jackknife 2 (J2).

For the cold season, the most abundant and frequent species were *Calanus pacificus*, *Rhincalanus nasutus*, *Pleuromamma gracilis*, *Clausocalanus jobei*, and *Aetideus armatus*. Together, these five species represented over 62% of the total copepod abundance and they were also the most frequent ones. As for the warm season, the most abundant and frequent species were instead *Nannocalanus minor*, *Rh. nasutus*, *Pl. gracilis*, *Scolecithrix danae*, and *Paracalanus aculeatus*. Together, these five species accounted for 60% of the total abundance of copepods. According to the SIMPER analysis, inter-zone dissimilarity was mainly influenced, for both seasons, by the abundances of *Ca. pacificus*, *N. minor*, *Rh. nasutus*, *Sc. danae*, *Cl. jobei*, and *Pl. gracilis*, together accounting for at least 20% of the contribution to the variation between zones.

Latitudinal variation of the composition and the ecological indices

The NMDS ordination gave a clear latitudinal pattern of the composition for the cold season, with increasing abundance of most species from the north to the entrance of the Gulf; there were not apparent differences between the SGC and the EGC (Fig. 3A). There was a much less clear latitudinal pattern in the warm season; the stations of the NGC and the CGC displayed a mixed arrangement, and the same occurred with the samples of the SGC and the EGC. However, the samples of the SGC-EGC zones conformed to two different subgroups: one given by the stations 1, 2, 7, and 63 (closer to the east coast of the gulf) and another by the stations 6, 54, and 58 (closer to the west coast) (Fig. 3B). The majority of the species with high contribution to the latitudinal variation for both seasons were, according to the SIMPER tests, considered as dominant species. These results were supported by the PERMANOVAs, the paired comparison results are displayed below (Tab. 1).

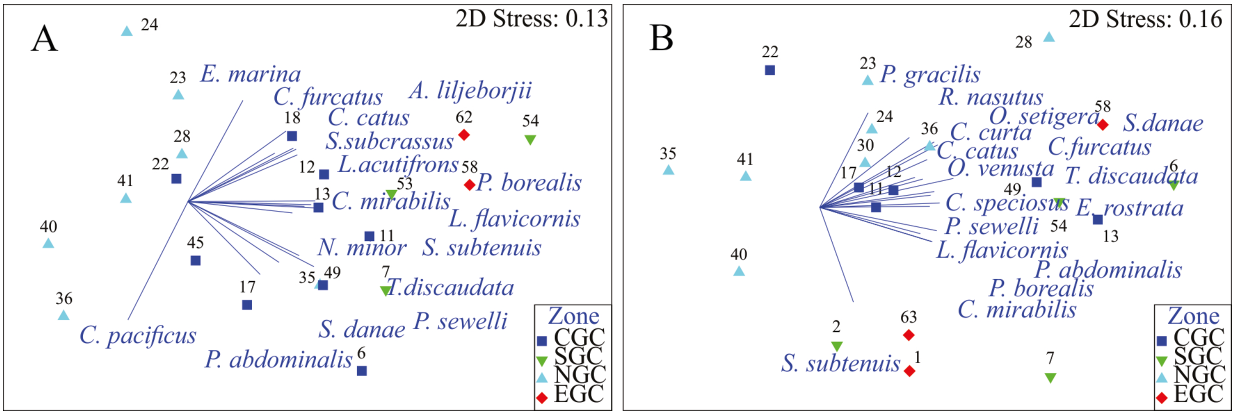

Figure 3. Latitudinal pattern of the copepod composition for the Gulf of California in 1985. NMDS ordination of the sampling stations of the CORTES 2 and 3 cruises: cold (**A**) and warm seasons (**B**). Vectors indicate the Pearson correlations between the dominant species abundance and the sampling stations. NGC, northern Gulf of California, CGC, central Gulf of California, SGC, southern Gulf of California, EGC, entrance of the Gulf of California.

Table 1. Paired comparisons between the four zones of the Gulf of California based on the composition data. Results from the PERMANOVA paired tests, expressed as P-values. Significant values are marked in boldface.

CORTES 2	**NGC**	**CGC**	**SGC**	**EGC**
NGC	-	-	-	-
CGC	**$P < 0.01$**	-	-	-
SGC	**$P < 0.01$**	$P > 0.05$	-	-
EGC	**$P < 0.05$**	**$P < 0.05$**	P > 0.05	-
CORTES 3	NGC	CGC	SGC	EGC
NGC	-	-	-	-
CGC	$P > 0.05$	-	-	-
SGC	**$P < 0.01$**	$P > 0.05$	-	-
EGC	**$P < 0.05$**	$P > 0.05$	$P > 0.05$	-

In regard to the ecological data, there was again a clear latitudinal pattern for the cold season, with the four zones conforming to distinct groups. The richness and the diversity strongly decreased from the north to the entrance of the Gulf (from 6 species at a single station in the NGC up to 35 species in the SGC), while the abundance was higher in the CGC (319,340 ind/10 m^3 on average) and lower in the NGC (203,764 ind/10 m^3 on average); the highest values were observed in the stations 18, 22, and 23 (closer to the west coast, CGC) (Fig. 4A). A similar richness-diversity latitudinal pattern was observed for the warm season, although the dissimilitude between the CGC, SGC, and the EGC zones were much less evident. The richness went from 11 species at a single station in the NGC and up to 35 species in the CGC. The abundance presented, on average, lower values in the NGC (84,493 ind/10 m^3), but the highest abundance was recorded in there, at station 28 (closer to the west coast) (Fig. 4B). On average, the highest abundance was recorded in the EGC (143,074 ind/10 m^3) during this season. The PERMANOVAs paired comparisons are presented below (Tab. 2).

Seasonal variation of the composition and the ecological indices

According to the SIMPER test, the species with the highest contribution to the differences between the two seasons were: *Ca. pacificus* (11.79%), *Rh. nasutus* (9.04%), *N. minor* (7.23%), *Aetideus armatus* (6.0%), *Pleuromamma gracilis* (5.16%), and *Cl. jobei* (4.79%). These six species accounted for 44 % of the contribution. The NMDS results indicate that the abundances of these species were higher during the cold season and more abundant towards the NGC zone (Fig. 5A). Finally, neither the diversity, nor the richness, shown any seasonal pattern, but the abundance was, in general, higher for the cold season (Fig. 5B). The PERMANOVA results indicated differences between the two seasons for the composition ($P < 0.005$), but not for the ecological data ($P > 0.05$), despite the seasonal change in abundance.

Environmental variables in relation to copepod distribution

A strong latitudinal pattern was observed for salinity in both seasons, gradually decreasing from the NGC towards the EGC. This pattern was stronger in the warm season, and the range of values was larger compared to the cold season; the CGC presented a higher average salinity during the cold season, similar to that recorded in the NGC (Fig. 6A, D). There was also strong latitudinal variation of temperature, but only during the cold season, with colder waters at the NGC, gradually heating towards the EGC (Fig. 6B); there was not any clear latitudinal temperature pattern during the warm season (Fig. 6E). We observed a longitudinal pattern in temperature for both seasons, with colder waters in the east coast for the cold season and colder waters in the west coast for the warm season (Fig. 6B, E). Finally, the spatial pattern of the dissolved oxygen was inverse to temperature, especially in the 5m-depth layer (Fig. 6C, F).

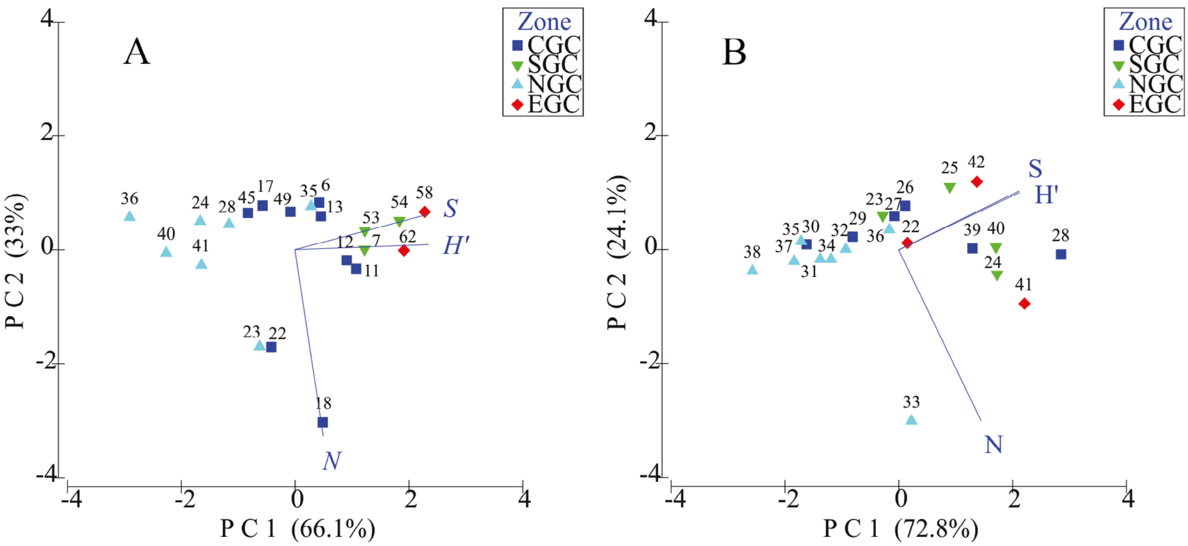

Figure 4. Latitudinal pattern of the copepod ecological indices in the Gulf of California in 1985. PCA ordination of the sampling stations of the CORTES 2 and 3 cruises: cold (**A**) and warm seasons (**B**). Vectors corresponds to the biological variables used in this study: S, richness, N, abundance, H', diversity. NGC, northern Gulf of California, CGC, central Gulf of California, SGC, southern Gulf of California, EGC, entrance of the Gulf of California.

Table 2. Paired comparisons between the four zones of the Gulf of California based in the ecological data. Results from the PERMANOVA paired tests, expressed as *P*-values. Significant values highlighted in boldface.

CORTES 2	**NGC**	**CGC**	**SGC**	**EGC**
NGC	-	-	-	-
CGC	**$P < 0.05$**	-	-	-
SGC	**$P < 0.01$**	$P > 0.05$	-	-
EGC	**$P < 0.05$**	**$P < 0.05$**	$P > 0.05$	-
CORTES 3	NGC	CGC	SGC	EGC
NGC	-	-	-	-
CGC	$P > 0.05$	-	-	-
SGC	**$P < 0.01$**	$P > 0.05$	-	-
EGC	**$P < 0.05$**	$P > 0.05$	$P > 0.05$	-

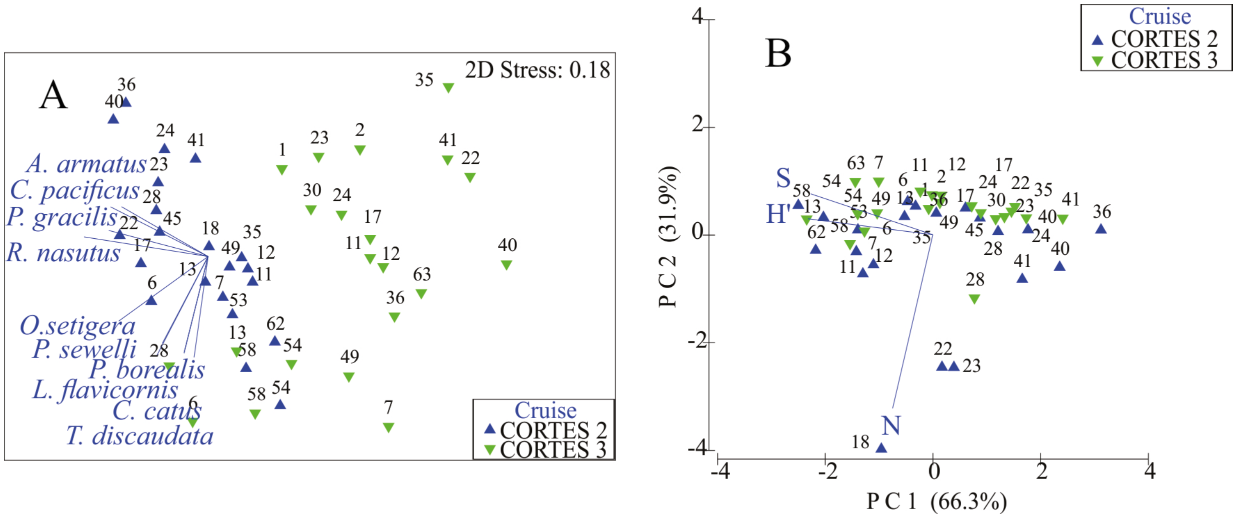

Figure 5. Seasonal variation of the composition (NMDS) (**A**) and the ecological indices (PCA) (**B**) in the Gulf of California in 1985: ordination of the sampling stations of the CORTES 2 and 3 cruises. Vectors correspond to the Pearson correlations between the dominant species abundance and stations (**A**) and to the ecological variables correlations (**B**): S, richness, N, abundance, H', diversity.

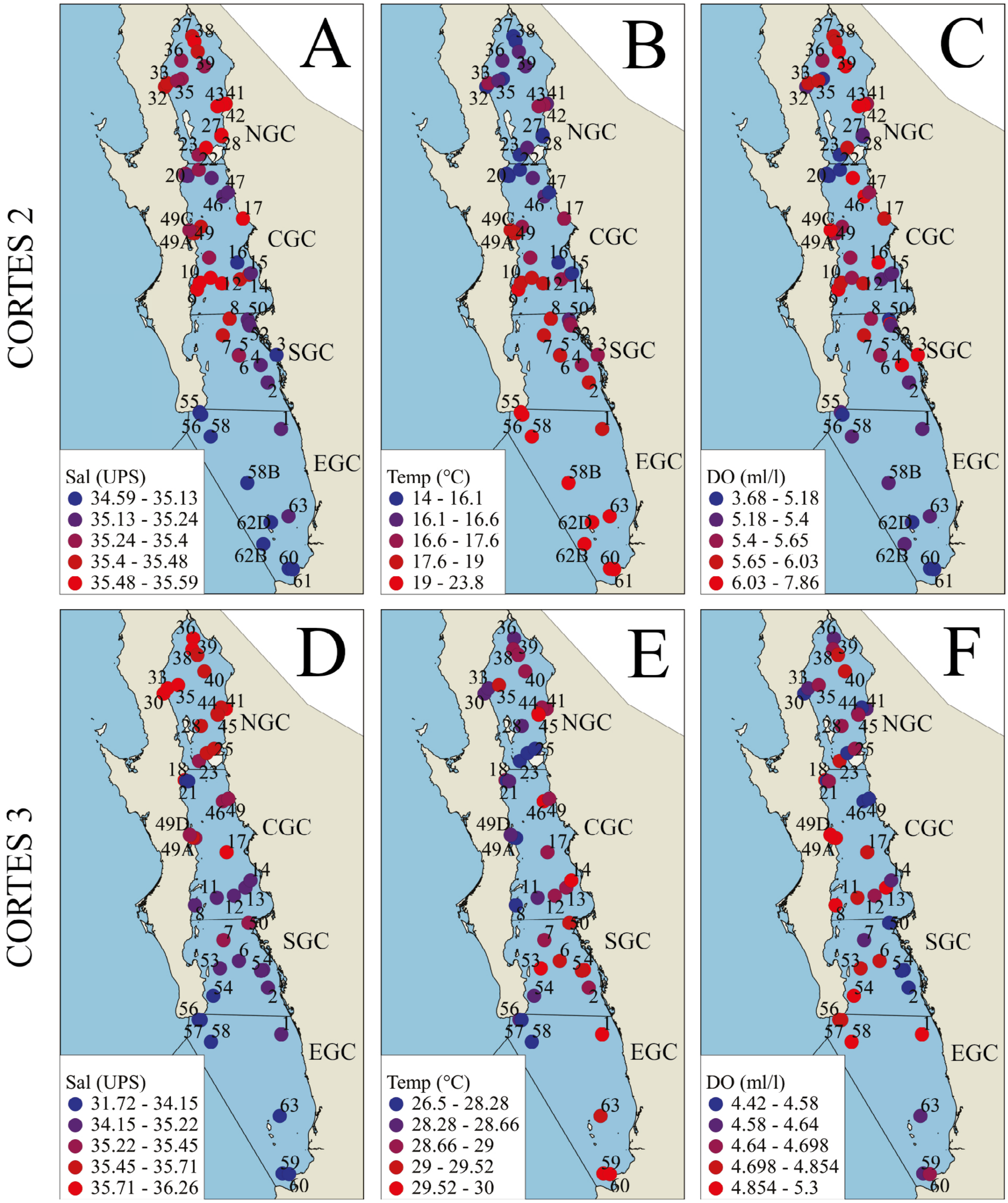

Figure 6. Maps showing the latitudinal variation of the environmental variables registered in the Gulf of California in 1985. Data were recorded during the CORTES 2 (cold season) (**A**, **B**, **C**) and the CORTES 3 (warm season) (**D**, **E**, **F**). The maps include the observed intervals of each variable for the first 5 m of depth: salinity (Sal), temperature (Temp) and dissolved oxygen (DO). NGC, northern Gulf of California, CGC, central Gulf of California, SGC, southern Gulf of California, EGC, entrance of the Gulf of California.

We observed no vertical variation of salinity for either season, but the range of the values was larger during the warm season (Fig. 7A). The strongest vertical (and seasonal) pattern was observed for temperature, with warmer waters in the 5 and 20 m-depth layers, abruptly decreasing at 75 m depth. This vertical stratification of the temperature was weaker during the cold season, and its average temperature in the first 20 meters was around 12 °C colder compared to the warm season temperatures (Fig. 7B). The dissolved oxygen showed less pronounced seasonal variation, but still it was significantly lower in the first two layers during the warm season compared to the cold season (Fig. 7C). The maximum, minimum and average values of each variable per depth level of both cruises are shown below (Tab. 3).

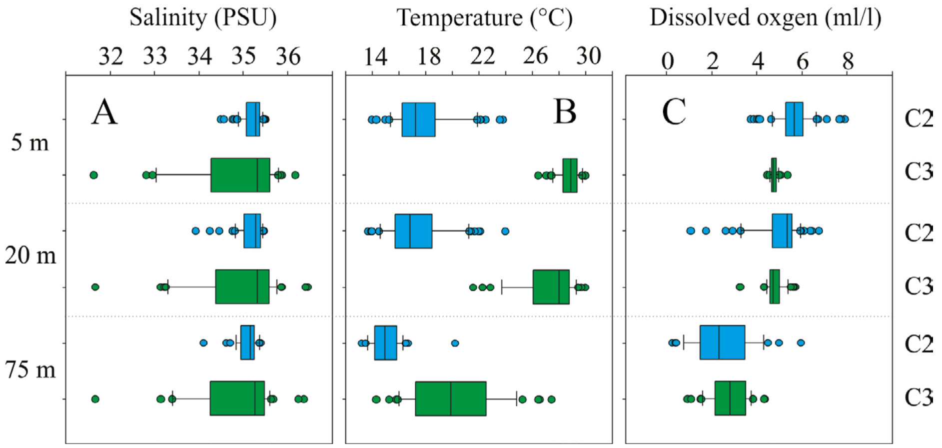

Figure 7. Vertical variation of the environmental variables registered in the Gulf of California in 1985: salinity (**A**), temperature (**B**) and dissolved oxygen (**C**) considering the records at 5, 20, and 75 m depth layers. The Boxplot graphics depict the observations in the cold (C2, blue) and the warm (C3, green) seasons.

Table 3. Maximum (max.), minimum (min.) and average (avg.) values of the environmental variables for the CORTES 2 and 3 cruises. Temperature expressed as °C, dissolved oxygen expressed as ml/l.

		Salinity	Temperature	Dissolved oxygen
CORTES 2				
5 m	max.	35.59	23.8	7.86
	min.	34.59	14	3.68
	avg.	35.29	17.76	5.59
20 m	max.	35.56	24	6.7
	min.	34.02	13.7	1.02
	avg.	35.26	17.31	4.91
75 m	max.	35.48	20.2	5.9
	min.	34.19	13.2	0.21
	avg.	35.17	15.04	2.45
CORTES 3				
5 m	max.	36.26	30	5.3
	min.	31.72	26.5	4.42
	avg.	34.89	28.78	4.70
20 m	max.	36.54	30	5.68
	min.	31.76	21.6	3.2
	avg.	35.01	27.30	4.72
75 m	max.	36.46	27.5	4.32
	min.	31.76	14.3	0.88
	avg.	34.98	20.04	2.67

The CCA analyses were statistically significant for the three depth layers ($P < 0.01$), and the variance inflation factor (VIF) values were maintained below 10 for all the variables, except for richness (VIF = 12.89) and diversity (VIF = 11.30) at 75 m depth, because of their strong correlation. The explanation (sum of the canonical eigenvalues over the inertia) of the first canonical eigenvalues was between 0.27 (for the 75 m-depth layer data) and 0.29 (for the 5 m-depth layer data). The main source of variation between the cold and warm seasons observed for the three bathymetric levels was temperature, which was negatively correlated with dissolved oxygen and abundance in the three analyses. Salinity contributed mostly to the latitudinal dissimilarity, and was negatively correlated with richness and diversity at both seasons and at the three bathymetric layers. Dissolved oxygen levels were positively correlated with abundance at the three depths and with richness and diversity at 20 m.

For the 5 m-depth CCA, the relationship between temperature and dissolved oxygen was inversely proportional. Both seasons were well separated and the species conformed to two well-defined groups, each associated with a season. The cold season species group was composed of, for example, *Aetideus armatus*, *Ca. pacificus*, *Heterorhabdus papilliger*, *Sc. danae*, and *Rh. nasutus*, while the warm season group was composed of *N. minor*, *Clausocalanus furcatus*, *Lucicutia pacifica*, *Labidocera trispinosa*, or *Pontella danae* (Fig. 8). The pattern was slightly different for the 20 m-depth CCA, where both the species and sampling stations groups were less defined; also, the relationship of temperature with salinity and dissolved oxygen was less inverse (Appendix - Fig. A1). Finally, for the 75 m-depth CCA, the temperature had stronger correlation with abundance, but neither the season, nor the species groups, were clearly defined (Appendix - Fig. A2). The correlation of each variable with the first two axes for the three levels of depth is presented below (Tab. 4).

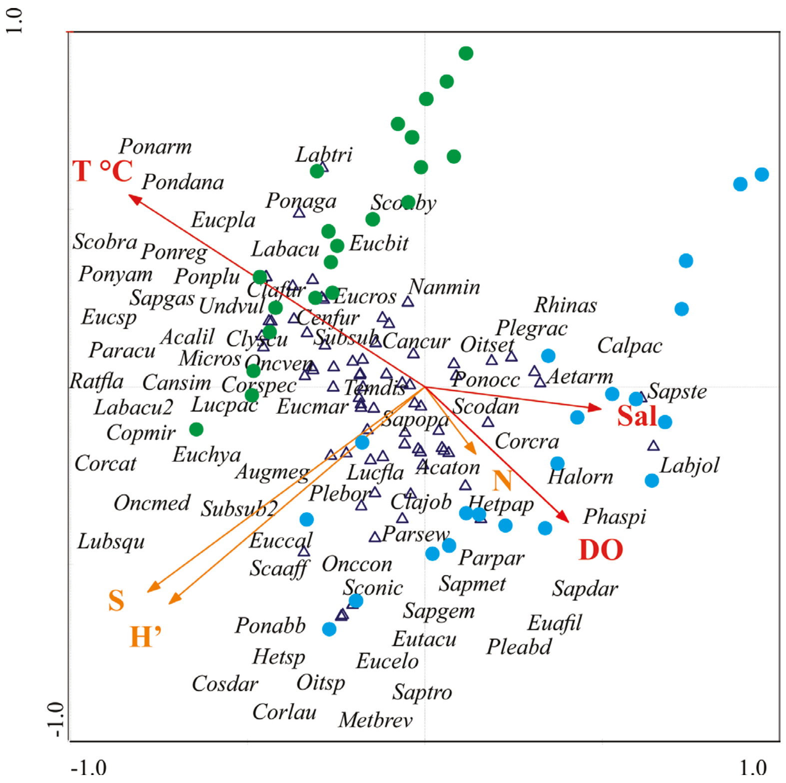

Figure 8. Influence of the environmental variables (red vectors; T° C-temperature, Sal-salinity, DO-dissolved oxygen) over the ecological indices (orange vectors; S-richness, H’-diversity, N-abundance) and the species composition (blue triangles) registered in the Gulf of California, in 1985. The CCA includes the stations of the cold (blue circles) and the warm (green circles) seasons. Results correspond to the environmental variables measured at a depth of 5 m.

Table 4. Correlation values for each environmental and ecological variable used in the CCA analyses. Each variable is correlated with the first two axes (AX1, AX2) of the three levels of depth (5, 20, and 75 m). S) richness, N) abundance, H’) diversity, Sal) salinity, Temp) temperature in °C, DO) dissolved oxygen.

Variable	AX1 (5 m)	AX2 (5 m)	AX1 (20 m)	AX2 (20 m)	AX1 (75 m)	AX2 (75 m)
S	-0.7473	-0.5213	-0.7577	-0.5201	0.8272	-0.3717
N	0.1365	-0.1712	0.1436	-0.1676	-0.1376	-0.1614
H’	-0.6899	-0.5516	-0.6986	-0.5557	0.7703	-0.3999
Sal	0.4746	-0.0564	0.4736	0.062	-0.6127	-0.1408
Temp	-0.7977	0.4877	-0.7883	0.4785	0.4445	0.5272
DO	0.3866	-0.3436	0.0693	-0.4709	-0.367	-0.3108

DISCUSSION

Taxonomic composition, richness, abundance and diversity

The observed copepod richness in this study was high, considering the short survey period. Past studies in the Gulf of California have shown high variability in their focus, sampling area, sampling period, and number of samples (see Appendix - Tab. A2). Lavaniegos et al. (2012) analyzed a large proportion of the zooplankton taxa and reported 24 copepod species in the Bahía de los Ángeles, Baja California. Jiménez-Pérez and Lara-Lara (1988) found 76 copepod species in the samples collected during March 1983 along the central and southern regions of the Gulf of California, with an average abundance of around 340,000 ind/10 m^3. Later, Lavaniegos-Espejo and Lara-Lara (1990) quantified the copepod abundance in the Gulf of California after the 1982-1983 ENSO event and reported around 560,000 ind/10 m^3. A complete checklist for the entire gulf, based on historic records, published in 1998 by Suárez-Morales and Gasca (1998) included 154 species, but some of these correspond to parasitic or benthic records. Gómez (2000; 2003; 2018a; 2018b; 2018c) have made several descriptions of coastal and marine benthic harpacticoids for the Gulf of California, although new pelagic copepod species are rarely described for this province. Palomares-García et al. (2013) reported a total of 52 species in a 2007 study of the central and northern Gulf of California and estimated their abundances to be between 100,000 and 500,000 ind/10 m^3. Álvarez-Tello et al. (2015) collected 33 species in a central Gulf of California embayment. Cruz-Hernández et al. (2018) reported 57 calanoid species in the central Gulf of California, and Beltrán-Castro et al. (2020) observed 49 copepod species for the Cabo Pulmo National Park, in the SW of the gulf, with a larger dominance of calanoids and an average abundance of 242,243 ind/10 m^3. Another review of historical records for the Bay of La Paz, in the SW gulf, indicated the presence of 146 species after a wide literature revision (Palomares-García et al. 2018). Based on these former works, we have estimated that the current number of pelagic species of copepods in the entire gulf is close to 160 species, although not all of these can be confirmed (see Appendix - Tab. A2). There is still a large unknown proportion of the Gulf of California waters below 200 m-depth, since most previous works have only surveyed the epipelagic layers. There are only a few works that explored the deep waters of the gulf, such as those of Wiebe et al. (2008) or Fleminger (1983), so there is a high chance that new records for this province can still be added.

Comparatively, the richness of epipelagic copepods along the west coast of the Baja California Peninsula, influenced by the California Current, is estimated to exceed 152 species (Hernández-Trujillo, 2004; López-Ibarra and Palomares-García, 2006). Information for the rest of western Mexico is scarce. Off the coast of Jalisco and Colima, around 82 species have been recorded (Kozak et al., 2014a; 2014b; 2018) while 72 species are known to occur off the coast of Oaxaca and Chiapas (Fernández-Álamo et al., 2000). Jiménez-Pérez (2016) reported 57 copepod species in Bahía de Banderas, located between Jalisco and Nayarit. Chen (1986) identified 63 species of copepods and their abundance, including some records for the mouth of the Gulf of California.

It is not easy to compare species lists of past papers, especially if their focus is not taxonomic. There are usually some incorrectly identified species in almost every non-taxonomic work, and their records could actually be assigned to other species, like for example *Acrocalanus longicornis* Giesbrecht, 1888 and *Acrocalanus gibber* Giesbrecht, 1888 records for the gulf (Lavaniegos-Espejo and López-Cortés, 1997; Gómez-Gutiérrez et al., 2014) could actually correspond to species of the genus *Scolecithricella* G.O. Sars, 1902. A similar problem occurs when only the genera are specified (e.g., Hernández-Nava and Álvarez-Borrego, 2013). The list presented in the most comparable work (Jiménez-Pérez and Lara-Lara, 1988) is actually very similar compared to our observations, except for some doubtful records, like *Spinocalanus* sp. or *Xanthocalanus* sp., probably corresponding to Lucicutiidae and Scolecithricidae, based on our observations. The general composition of the copepods in the gulf seems to be, however, very stable throughout the years.

The average abundance values recorded for the warm season samples were low if compared to the most similar works (Jiménez-Pérez and Lara-Lara, 1988; Lavaniegos-Espejo and Lara-Lara, 1990; Palomares-García et al., 2013; Coria-Monter et al., 2020), but close to the expected according to the works of Chen (1986) and López-Ibarra et al. (2014) in the Eastern Tropical Pacific, and higher than the reported out of the gulf (e.g., Kozak et al., 2018). The average copepod abundance recorded for the cold season (265,649 ind/10 m^3) was significantly higher, and the highest recorded density (1,021,076 ind/10 m^3) was similar to the values that can be observed in temperate and cold waters (see Spinelli et al., 2016; Thompson et al., 2013). Usually, the productivity is expected to be lower during an El Niño event, since the high productivity tends to be associated with colder and saltier waters, as pointed by Santamaría-del-Angel et al. (1994), but the Gulf of California seems to behave inversely compared to other provinces in the ETP (Valdéz-Holguín and Lara-Lara, 1987). During the 1982–1983 El Nino event, the phytoplankton productivity was actually increased and the zooplankton abundance didn't significatively decrease, but there was a change in the copepod composition (Valdéz-Holguin and Lara-Lara, 1987; Jiménez-Pérez and Lara-Lara, 1988). Our lower observed abundances could then be related to the weak effect of La Niña in 1985, but also to the later consequences caused by the change in the copepod composition during El Niño 1982–1983.

Latitudinal and seasonal copepod variation in the Gulf of California

The spatial variation of copepods was similar to the recognized distribution patterns for other pelagic groups (Brinton and Townsend, 1980; Brinton et al., 1986; Urias-Leyva et al., 2018; Quiroz-Martínez et al., 2023) and copepods in other years (Jiménez-Pérez and Lara-Lara, 1988; Lavaniegos-Espejo and Lara-Lara, 1990; Palomares-García et al., 2013). This can be attributed to the oceanographic characteristics in the gulf and the general spatial distribution of phytoplankton (Santamaría-del-Angel and Alvarez-Borrego, 1994; Mercado-Santana et al., 2017; Robles-Tamayo et al., 2020). From these studies on phytoplankton, we know that the largest abundance in the gulf is present in the NGC, and it gradually decreases towards the EGC, an inverse pattern to the copepod abundance here reported. The diversity of copepods, at least in the Eastern Tropical Pacific, is usually higher in oligotrophic waters than in more productive waters (Fernández-Álamo and Färber-Lorda, 2006), so the lower diversity observed at the NGC compared to the rest of the gulf is not unexpected. A parabolic pattern for the zooplankton richness of the Gulf of California was noticed by Quiroz-Martínez et al. (2023), describing a decrease in the richness both towards the NGC and the SGC. This was predicted by the mid-domain effect, produced when the species ranges of distribution overlaps in a geometrical middle, resulting in a unimodal curve for the richness (Colwell and Lees, 2000).

Differences between the four zones were clear, considering both the environmental and the ecological data, only during the cold season, with statistically significant differences between all the zones ($P < 0.05$), except for the comparison between the CGC and the SGC. The NGC remained as a different zone in the gulf, considering both composition and ecologic data in the cold season ($P < 0.05$ vs. CGC, SGC, EGC), but it was similar to the CGC ($P > 0.05$) in the warm season. The absence of statistically significant differences between the CGC and the SGC in both seasons in terms of composition and ecology are unexpected when compared to the work of Jiménez-Pérez and Lara-Lara (1988). There was no difference between the EGC and the SGC in any season, and the EGC was different compared to the CGC only in the cold season ($P < 0.05$), considering both composition and diversity. This lack of latitudinal pattern of copepods in the Gulf of California during the summer is probably related to the seasonal change in the water masses inside the gulf, with a stronger inflow of warm tropical waters to the inner gulf (see Álvarez-Borrego and Schwartzlose, 1979; Portela et al., 2016).

The east-west gradient pattern observed for the composition, temperature and dissolved oxygen can be explained by two different scenarios: either the seasonally reversing winds and sea surface circulation cause this by upwelling events, or the inflow of TSW into the east coast and the outflow of GCW from the west coast (Portela et al., 2016) is the main cause of this effect. It is necessary to sample a larger number of stations that allows comparison in a more efficient way of how different the western copepod community is compared to the eastern community. This seasonal pattern can be compared to that observed in the gulf by Palomares-García et al. (2013), who showed a seasonal shift in the composition, related to the functional structure of the phytoplankton. They also observed dominance of larger copepod species in winter, mostly herbivores, and of smaller, mostly carnivorous species in summer, and also noticed the species composition gradient between the NGC and the CGC.

Environmental influence on copepod richness, abundance, and diversity

Changes in taxonomic groups reflect the large environmental variation in their ecosystems (Hernández-Trujillo et al., 2010). Copepods and other zooplanktonic groups are affected in different ways by seasonal changes. Dominance of certain copepod groups may vary from one season to another, sometimes being reduced enough to become rare, giving place to biological successions (Fulton, 1984; Stevens and Campbell, 2022). Seasonal and interannual abundance variation has been studied for some species like *Acartia clausi* Giesbrecht, 1889 and *Calanus finmarchicus* (Gunnerus, 1770), both showing marked temporal patterns in their distribution (Valdés et al., 2022). If we compare the composition observed in the present study with some of the most similar works for the Gulf of California (Appendix – Tab. A2), the dominant species are usually the same, despite the zone, season or survey period. The largest difference in the composition between zones, seasons and years are shown for the infrequent or less abundant species, probably due to their higher sensitivity to environmental changes.

Latitudinal patterns of copepod richness and diversity have been positively correlated with temperature variation and dissolved oxygen concentration (Rombouts et al., 2009; Ashlock et al., 2021) but, for this scale, we observed no correlation between the diversity and temperature at any depth. Rombouts et al. (2009) described a positive latitudinal correlation between salinity and diversity, an inverse pattern to that observed in this province (Ulate et al., 2016). Salinity is probably not directly driving the latitudinal copepod variation in the Gulf of California, but the phytoplankton abundance and its size structure might be. The latitudinal and seasonal differences for primary productivity in the gulf (decreasing from the NGC to the EGC, higher during the winter) (Santamaria-del-Angel and Alvarez-Borrego, 1994; Mercado-Santana et al., 2017; Robles-Tamayo et al., 2020) concur with the copepod abundance and diversity spatial patterns, and the size of the phytoplankton cells (micro-phytoplankton dominance in the CGC, nano-phytoplankton dominance in the SGC) (Valdéz-Holguín and Lara-Lara, 1987; Lara-Lara et al., 1993) seems to be linked to copepod composition. The influence of the salinity on the phytoplankton has different effects, including changes in nutrient availability (Sew and Todd, 2020).

The seasonal temperature shift, together with the seasonal change of the productivity in the gulf, can explain the seasonal change in both composition and abundance. The most abundant and frequent species herein registered in the cold season are considered to be large-sized herbivores, such as *Rh. nasutus*. This is a widespread species with a wide depth range and resistance to low oxygen concentrations and starvation (Schnack-Schiel et al., 2008). This species has been observed to be a cryptic species complex, with inter-population differences that don't match their distribution (Goetze, 2003). *Calanus pacificus* is considered to prefer temperate waters (López-Ibarra and Palomares-García, 2006; Engström-Öst et al., 2019), although its abundance can also be associated with warmer waters (Fisher et al., 2020; Ashlock et al., 2021). This species is highly abundant and frequent in waters influenced by the California current (Hernández-Trujillo, 1991), and is also a resistant species when oxygen concentrations are low (Engström-Öst et al., 2019; Wyeth et al., 2022). *Pl. gracilis* has shown a wide range of tolerance to dissolved oxygen values, and it has been observed to be a dominant species in relation to other *Pleuromamma* Giesbrecht in Giesbrecht and Schmeil, 1898 species (Jayalakshmy et al., 2008).

The warm season was characterized by smaller species, like the carnivorous pontellids and corycaeids, or the small herbivore *N. minor*, a dominant species in this season. This species has a wide distribution and has been associated with large thermocline conditions, where its abundance can be considerably high (Cruz-Hernández et al., 2018). For the Gulf of Tehuantepec, pontellids have been described as a very versatile group, easily adapting to changes in salinity and temperature

(Álvarez-Silva et al., 2003). The relative higher diversity and abundance of pontellids observed for the warm season can be explained by their significant association with lower phytoplankton productivity, due to their diet type, mostly carnivorous (Battuello et al., 2017). Corycaeids are well known as predators (e.g., Landry et al., 1985; Turner et al., 1984) and are considered to have great adaptative capacity against changing conditions (Bjönberg, 1981; Suárez-Morales, 1989). Spinelli et al. (2016) observed that the higher solar radiation and temperature in summer caused an increase in carnivorous species, correlated with a decrease in diatom abundance and an increase in flagellate abundance, while the winter is characterized by the dominance of herbivorous species. This aligns well with the findings of Palomares-García et al. (2013) concerning copepod composition of the Gulf of California.

Dissolved oxygen concentrations seemed to have a noticeable effect on the variation of composition at the three layers of depth. Some species like *Haloptilus ornatus*, *Sapphirina gema*, *Oncaea conifera*, *Heterorhabdus papilliger*, and *Pleuromamma borealis* exhibited a distribution related to higher dissolved oxygen concentrations, while other species like *Pontella agassizi*, *Pontellopsis armata*, *Pontellina plumata*, *Labidocera trispinosa*, and *Euchaeta plana* showed higher affinity for lower dissolved oxygen concentrations. Most of the dominant species, like *Ca. pacificus*, *Rh. nasutus*, *Ae. armatus*, and *Pl. gracilis*, were associated with saltier and colder waters, with higher concentrations of dissolved oxygen. Other dominant species, like *N. minor* or *Ce. furcatus*, were associated with fresher and hotter waters, lower in dissolved oxygen concentrations.

CONCLUSIONS

The taxonomic composition was similar to previously published research for the Gulf of California, except for the differences in some infrequent species. There was a clear latitudinal pattern of the richness and diversity for the cold season, but not for the warm season, due to the seasonal changes in the water masses of the gulf. The NGC was the only zone that remained different from the rest of the gulf during both seasons. The CGC and the SGC were not different in any season, and the SGC was not different from the EGC either. The east and west coasts of the SGC and the EGC were different in terms of composition, because of the seasonal changes in the sea circulation, noticeable by the temperature spatial pattern. The cold and warm seasons were different in terms of composition, but similar in terms of diversity; the abundance was higher in the cold season. Salinity variation was strongly correlated with the latitudinal variation of richness and diversity, probably because of its influence on phytoplankton abundance and size structure. Temperature (inversely correlated with dissolved oxygen) had a larger effect on composition and abundance between the two seasons, matching the seasonal change in phytoplankton abundance. The observed richness was high, but the abundance was low if compared to that observed during the 1982–1983 El-Niño, probably because of the later effects of the change in the composition caused by this event.

AKNOWLEDGMENTS

Special thanks to the Posgrado en Ciencias del Mar y Limnología, UNAM, for providing the needed facilities and materials to conclude this research as part of this postgraduate program, as is required to obtain the doctoral degree for Karl Velázquez. We greatly appreciate the scholarship given by the CONACYT; it made this work possible. We also appreciate the hints provided by Samuel Gómez and Eduardo Suárez Morales for the manipulation and identification of the material.

REFERENCES

Álvarez-Borrego S 1983. Gulf of California. p. 427–449. In: Ketchum BH (Ed.), Estuaries and Enclosed Seas. Amsterdam, Netherlands, Elsevier Scientific Publications.

Álvarez-Borrego S and Galindo LA 1974. Hidrología del Alto Golfo de California-I. Condiciones durante otoño. *Ciencias marinas*, 1(1): 46–64. https://doi.org/10.7773/cm.v1i1.248

Álvarez-Borrego S and Lara-Lara JR 1991. The physical environment and primary productivity of the Gulf of California. P. 565–567. In: Simoneit BRT; Dauphin JJA; Mercado-Santana et al. (Ed.), The Gulf and Peninsular Province of the Californias. American Association of Petroleum Geologists.

Álvarez-Borrego S and Schwartzlose, LA 1979. Water masses of the Gulf of California. *Ciencias Marinas*, 6: 43–63. https://doi.org/10.7773/cm.v6i1.350

Álvarez-Silva C; Arce MGM and De Lara-Isassi G 2003. Familia Pontellidae (Crustacea: Copepoda) en la Bahía La Ventosa, Oaxaca, México: Sistemática y ecología. *Revista de Biología Tropical*, 51(3): 737–742.

Álvarez-Tello FJ; López-Martínez J; Funes-Rodríguez R; Lluch-Cota DB; Rodríguez-Romero J and Flores-Coto C 2015. Composición, estructura y diversidad del mesozooplancton en Las Guásimas, Sonora, un sitio Ramsar en el Golfo de California, durante 2010. *Hidrobiológica*, 25(3): 401–410.

Angulo-Campillo O; Aceves-Medina G and Avedaño-Ibarra R 2011. Holoplanktonic mollusks (Mollusca: Gastropoda) from the Gulf of California, México. *Journal of Species Lists and Distribution*, 7(3): 337–342. https://doi.org/10.15560/7.3.337

Argote ML; Amador A; Lavín MF and Hunter JR 1995. Tidal dissipation and stratification in the Gulf of California. *Journal of Geophysics Research*, 100: 16103–16118. https://doi.org/10.1029/95JC01500

Ashlock L; García-Reyes M; Gentemann C; Batten S and Sydeman W 2021. Temperature and patterns of occurrence and abundance of key copepod taxa in the Northeast Pacific. *Frontiers in marine science*, 8. https://doi.org/10.3389/fmars.2021.670795

Badan-Dangon A; Koblinsky CJ and Baumgartner T 1985. Spring and summer in the Gulf of California: observations of surface thermal patterns. *Oceanologica Acta*, 8(1): 13–22.

Battuello M; Mussat-Sartor R; Brizio P; Nurra N; Pessani D; Abete MC and Squadrone S 2017. The influence of feeding strategies on trace element bioaccumulation in copepods (Calanoida). *Ecological Indicators*, 74: 311–320. https://doi.org/10.1016/j.ecolind.2016.11.041

Beltrán-Castro JR; Hernández-Trujillo S; Gómez-Gutiérrez J; Trasviña-Castro A; González-Rodríguez E and 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): e-104215. https://doi.org/10.1016/j.csr.2020.104215

Björnberg TA 1981. Copepoda. p. 587–679. In: Boltovskoy D (Ed). Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino. Mar del Plata, Argentina, Publicación especial INIDEP.

Brinton E and Townsend AW 1980. Euphasids in the Gulf of California – The 1957 cruises. *CalCOFI Reports*, 21: 211–236.

Brinton E; Fleminger A and Siegel-Causey D 1986. The temperate and tropical planktonic biotas of the Gulf of California. *CalCOFI Reports*, 27: 228–266.

Brusca RC; Findley LT; Hastings PA; Hendrickx ME; Torre J and van der Heiden AM 2005. Macrofaunal diversity in the Gulf of California. p. 179–203. In: Cartron JLE; Ceballos G and Felger RS (Eds.), Biodiversity, ecosystems, and conservation in northern Mexico. London, Oxford University Press.

Castro R; Lavín MF and Ripa P 1994. Seasonal heat balance in the Gulf of California. *Journal of Geophysical Research*, 99(C2): 3249–3261. https://doi.org/10.1029/93JC02861

Castro R; Mascarenhas AS; Durazo R and Collins CA 2000. Variación estacional de la temperatura y salinidad en la entrada del golfo de California, México. *Ciencias Marinas*, 26(4): 561–583. https://doi.org/10.7773/cm.v26i4.621

Chen YQ 1986. The vertical distribution of some pelagic copepods in the Eastern Tropical Pacific. *CalCOFI Reports*, 27: 205–227.

Colwell RK and Lees DC 2000. The mid-domain effect: geomet- ric constraints on the geography of species richness. *Trends in Ecology and Evolution*. 15(2): 70–76. https://doi.org/10.1016/S0169-5347(99) 01767-X

Coria-Monter E; Monreal-Gómez MA; Salas de León DA and Durán-Campos E 2020. Zooplankton abundance during summer in the Bay of La Paz (southwestern Gulf of California, Mexico). *Latin American Journal of Aquatic Research*, 48(5): 794–805. https://doi.org/10.3856/vol48-issue5-fulltext-2515

Cruz-Hernández J; Sánchez-Velasco L; Beier E, Godínez VM and Barton ED 2019. Distribution of calanoid copepods across the mesoscale frontal zone of tropical-subtropical convergence off México. *Deep-Sea Research Part II*. https://doi.org/10.1016/j.dsr2.2019.104678

Cruz-Hernández J; Sánchez-Velasco L; Godínez VM; Beier E; Palomares-García JR; Barton ED and Santamaría-del-Angel E 2018. Vertical distribution of calanoid copepods in a mature cyclonic eddy in the Gulf of California. *Crustaceana*, 91(1): 63–84. https://doi.org/10.1163/15685403-00003751.

Durazo R; Gaxiola-Castro G; Lavaniegos B; Castro-Valdéz R; Gómez-Valdés J and Mascarenhas Jr. ADS 2005. Oceanographic conditions west of the Baja California coast, 2002–2003: A weak El Niño and subarctic water enhancement. *Ciencias Marinas*, 31(3): 537–552. https://doi.org/10.7773/cm.v31i3.43

Engström-Öst J; Glippa O; Feely RA; Kanerva M; Keister JE; Alin SR; Carter BR; McLaskey AK; Vuori KA and Bednaršek N 2019. Eco-physiological responses of copepods and pteropods to ocean warming and acidification. *Scientific Reports*, 9(1): e-4748. https://doi.org/10.1038/s41598-019-41213-1

Fernández-Álamo MA and Färber-Lorda J 2006. Zooplankton and the oceanography of the eastern tropical Pacific: A review. *Progress in Oceanography*, 69(2–4): 318–359. https://doi.org//10.1016/j.pocean.2006.03.003.

Fernández-Álamo MA; Sanvicente-Añorve L and Alameda-de-la-Mora G 2000. Copepod assemblages in the Gulf of Tehuantepec, Mexico. *Crustaceana*, 73(9): 1139–1153. https://doi.org/10.1163/156854000505137.

Fisher J; Kimmel D; Ross T; Batten S; Bjorkstedt E; Galbraith M; Jacobson K; Keister J; Sastry A; Suchy K; Zeman S and Perry MI 2020. Copepod responses to, and recovery from, the recent marine heatwave in the Northeast Pacific. *North Pacific Marine Science Organization*, 28(1): 65–71.

Fleminger A 1967. Taxonomy, distribution and polymorphism in the *Labidocera jollae* group with remarks on evolution within the group (Copepoda: Calanoida). *Proceedings of the United States National Museum*, 120(3567): 1–61. https://doi.org/10.5479/si.00963801.120-3567.1

Fleminger A 1975. Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera*. *Estuarine Research*, 1: 392–419.

Fleminger A 1983. Description and phylogeny of *Isaacsicalanus paucisetus* n. gen., n. sp. (Copepoda: Calanoida: Spinocalanidae) from an east Pacific hydrothermal vent site. *Proceedings of the Biological Society of Washington*, 96(4): 605–622.

Fulton RS 1984. Distribution and community structure of estuarine copepods. *Estuaries*, 7(1): 38–50. https://doi.org/10.2307/1351955

García-Rodríguez FJ; Ponce-Diaz G; Muñoz-García I; González-Armas R and Pérez-Enriquez R 2008. Mitochondrial DNA markers to identify commercial spiny lobster species (*Panulirus* spp.) from the *Pacific coast of Mexico: an application on phyllosoma larvae. Fishery Bulletin*, 106(2): 204–212.

Gasca R; Suárez-Morales E and Haddock SHD 2015. *Sapphirina iris* Dana, 1849 and *S. sinuicauda* Brady, 1883 (Copepoda, Cyclopoida): predators of salps in Monterey Bay and the Gulf of California. *Crustaceana*, 88(6): 689–699. https://doi.org/10.1163/15685403-00003438

Gilbert JY and Allen WA 1943. The phytoplankton of the Gulf of California obtained by the E.W. Scripps in 1939 and 1940. *Journal of Marine Research*, 5: 89–110.

Goetze E 2003. Cryptic speciation on the high seas; global phylogenetics of the copepod family Eucalanidae. *Proceedings of the Royal Society of London*, 270: 2321–2331. https://doi.org/10.1098/rspb.2003.2505

Gómez S 2000. A new genus, a new species and a new record of the family Darcythompsidae Lang, 1936 (Copepoda: Harpacticoida) from the Gulf of California, *Mexico. Zoological Journal of the Linnaean Society*, 129: 515–536. https://doi.org/10.1111/j.1096-3642.2000.tb00615.x

Gómez S 2003. Three new species of *Enhydrosoma* and a new record of *Enhydrosoma lacunae* (Copepoda: Harpacticoida: Cletodidae) from the Eastern Tropical Pacific. *Journal of Crustacean Biology*, 23(1): 94–118. https://doi.org/10.1163/20021975-99990320

Gómez S 2018a. New species of the genus *Mesocletodes* Sars, 1909 from the deep Gulf of California (Copepoda, Harpacticoida). *ZooKeys*, 751: 75–112. https://doi.org/10.3897/zookeys.751.20387

Gómez S 2018b. Two new deep-sea species of Argestidae and Ameiridae (Copepoda: Harpacticoida) from the Eastern Mexican Pacific and Gulf of California, with proposal of a new genus of the family Argestidae. *Journal of Natural History*, 52(41-42): 2613–2638. https://doi.org/10.1080/00222933.2018.1546915

Gómez S 2018c. New species of *Eurycletodes* Sars, 1909 and *Odiliacletodes* Soyer, 1964 from the deep Gulf of California (Copepoda, Harpacticoida, Argestidae). *ZooKeys*, 764: 1–25. https://doi.org/10.3897/zookeys.764.24511

Gómez S and Yáñez-Rivera B 2023. On new species of three genera of Zosimeidae Seifried, 2003 (Copepoda: Harpacticoida) from the deep sea of the Gulf of California and Gulf of Mexico, with notes on the phylogeny of the family and on the species groups of *Zosime* Boeck, 1873 †. *Diversity*, 15: 363. https://doi.org/10.3390/d15030363

Gómez-Gutiérrez J; Funes-Rodríguez R; Arroyo-Ramírez K; Sánchez-Ortíz CA; Beltrán-Castro JR; Hernández-Trujillo S; Palomares-García R; Aburto-Oropeza O and Ezcurra E 2014. Oceanographic mechanisms that possibly explain dominance of neritic-tropical zooplankton species assemblages around the Islas Marías Archipelago, Mexico. *Latinoamerican Journal of Aquatic Research*, 42(5): 1009–1034. https://doi.org/10.3856/vol42-issue5-fulltext-7

González-Acosta AF; Monsalvo-Flores AE; Tovar-Ávila J; Jiménez-Castañeda MF; Alejo-Plata MC and De la Cruz-Agüero G 2021. Diversity and conservation of Chondrichthyes in the Gulf of California. *Marine Biodiversity*, 51(46): 1–17. https://doi.org/10.1007/s12526-021-01186-9

Hamilton W 1961. Origin of the Gulf of California. *Geological Society of America Bulletin*, 72: 1307–1318. https://doi.org/10.1130/0016-7606(1961)72[1307:OOTGOC]2.0.CO;2

Hastings PA; Findley LT and Van der Heiden AM 2010. Fishes of the Gulf of California. p. 96–118. In: Brusca R (Ed.), The Gulf of California Biodiversity and Conservation. Tucson, Arizona, University of Arizona Press.

Hendrickx ME 1987. *Podochela casoae*, new species (Brachyura, Majidae) from the continental shelf of the Gulf of California, Mexico, with a note on ecology and distribution of *Podochela* in the Eastern Pacific. *Journal of Crustacean Biology*, 7(4): 764–770. https://doi.org/10.1163/193724087X00496

Hendrickx ME and Estrada-Navarrete FD 1994. Temperature related distribution of *Lucifer* typus (Crustacea: Decapoda) in the Gulf of California. *Revista de Biología Tropical*, 42(3): 581–586.

Hendrickx ME; Brusca RC; Cordero M and Ramírez G 2007. Marine and brackish-water molluscan biodiversity in the Gulf of California, Mexico. *Scientia Marina*, 71(4): 637–647. https://doi.org/10.3989/scimar

Hernández-Nava MF and Álvarez-Borrego S 2013. Zooplankton in a whale shark (*Rhincodon typus*) feeding area of Bahía de los Ángeles (Gulf of California). *Hidrobiológica*, 23(2): 198-208.

Hernández-Trujillo S 1991. Latitudinal variation of copepod diversity on the west coast of B.C.S., Mexico 1982-1984. *Ciencias marinas*, 17(4): 83–103. https://doi.org/10.7773/cm.v17i4.843

Hernández-Trujillo S; Esqueda-Escárcega G and Palomares-García R 2010. Variabilidad de la abundancia de zooplancton en Bahía Magdalena Baja California Sur, México (1997-2001). *Latinoamerican Journal of Aquatic Research*, 38(3): 438–446. https://doi.org/10.3856/vol38-issue3-fulltext-8

Hernández-Trujillo S; Palomares-García R; López-Ibarra G.A; Esqueda-Escárcega G and Pacheco-Chávez R 2004. Riqueza específica de copépodos en Bahía Magdalena, Baja California Sur, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología*, 75(2): 253–270.

Humes AG 1987. Copepoda from deep-sea hydrothermal vents and cold seeps. *Bulletin of Marine Science*, 41(3): 645–788. https://doi.org/10.1007/978-94-009-3103-9_63

Jalayakshhmy KV; Saraswathy M and Maheswari N 2008. Effect of water quality parameters on the distribution of *Pleuromamma* (Copepoda–Calanoida) species in the Indian Ocean: a statistical approach. *Environmental Monitoring and Assessment*, 155: 373–392. https://doi.org/10.1007/s10661-008-0441-0

Jiménez-Pérez LC 2016. Estructura de las comunidades de copépodos de Bahía de Banderas durante La Niña 2008-2009 y su transición hacia El Niño 2009-2010. *Revista Bio Ciencias*, 4(2): 82–103. https://doi.org/10.15741/revbio.04.02.02

Jiménez-Pérez LC and Lara 1988. Zooplankton biomass and copepod community structure in the Gulf of California during the 1982-1983 El Niño event. *CalCOFI Repository*, 29, 122–128.

Kozak ER; Franco-Gordo C; Suárez-Morales E and Palomares-García R 2014a. 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. https://doi.org/10.3354/meps10811

Kozak ER; Suárez-Morales E; Palomares-García R and Franco-Gordo MC 2014b. Copépodos de la costa sur de Jalisco y Colima. p. 79–91. In: Franco-Gordo MC (Ed.), Inventario de biodiversidad de la costa sur de Jalisco y Colima. México, Universidad de Guadalajara. https://doi.org/10.13140/2.1.2662.7527

Kozak ER; Olivos-Ortiz A; Franco-Gordo C and 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(4): 1449–1468. https://doi.org/10.15517/rbt.v66i4.32058

Landry MR; Lehner-Fournier JM and Fagerness VL 1985. Predatory feeding behavior of the marine cyclopoid copepod *Corycaeus anglicus*. *Marine Biology*, 85: 163–169. https://doi.org/10.1007/BF00397435

Lara-Lara JR; Millán-Núñez R; Lara-Osorio JL and Bazán-Guzmán C 1993. Phytoplankton productivity and biomass by size classes, in central Gulf of California during spring, 1985. *Ciencias Marinas*, 19(2): 137–154. https://doi.org/10.7773/cm.v19i2.932.

Lavaniegos-Espejo BE and Lara-Lara JR 1990. Zooplankton of the Gulf of California after the 1982-1983 El Niño event: biomass, distribution and abundance. *Pacific Science*, 44(3): 297–310.

Lavaniegos-Espejo BE and López-Cortés D 1997. Fatty Acid Composition and Community Structure of Plankton from the San Lorenzo Channel, Gulf of California. *Estuarine, Coastal and Shelf Science*, 45: 845–854. https://doi.org/10.1006/ecss.1997.0245.

Lavaniegos-Espejo BE and González-Navarro E 1999. Cambios en la comunidad de copépodos durante el ENSO 1992-93 en el Canal de San Lorenzo, Golfo de California. *Ciencias Marinas*, 25(2): 239–265. https://doi.org/10.7773/cm.v25i2.663

Lavaniegos-Espejo BE; Heckel G and Ladrón de Guevara P 2012. Seasonal variability of copepods and cladocerans in Bahía de los Ángeles (Gulf of California) and importance of *Acartia clausi* as food for whale sharks. *Ciencias Marinas*, 38(1A): 11–30. https://doi.org/10.7773/cm.v38i1A.2017

Lavín MF and Marinone SG 2003. An overview of the physical oceanography of the Gulf of California. pp. 173–204. In: Velasco Fuentes OU, Sheinbaum J and Ochoa J (Eds.), Nonlinear Processes in Geophysical Fluid Dynamics. Dordrecht, Netherlands, Kluwer Academic Publishers. https://doi.org/10.1007/978-94-010-0074-1.

Lavín MF; Palacios-Hernández E and Cabrera C 2003. Sea surface temperature anomalies in the Gulf of California. *Geofísica Internacional*, 42(3): 363–375. https://doi.org/10.22201/igeof.00167169p.2003.42.3.956.

Lavín MF; Gaxiola-Castro G; Robles JM and Richter K 1995. Winter water masses and nutrients in the northern Gulf of California. *Journal of Geophysical Research*, 100(C5): 8587–8605. https://doi.org/10.1029/95JC00138

Lavín MF; Durazo R; Palacios E; Argote ML and Carrillo L 1997. Lagrangian Observations of the Circulation in the Northern Gulf of California. *Journal of Physical Oceanography*, 27: 2298–2305. https://doi.org/10.1175/1520-0485

Lavín MF; Castro R; Beier E; Cabrera C; Godínez VM and Amador-Buenrostro A 2014. Surface circulation in the Gulf of California in summer from surface drifters and satellite images (2004–2006), *Journal of Geophysical Research: Oceans*, 119: 4278–4290. https://doi.org/10.1002/2013JC009345

López-Ibarra GA and Palomares-García R 2006. Estructura de la comunidad de copépodos en Bahía Magdalena, México, durante El Niño 1997-1998. *Revista de Biología Marina y Oceanografía*, 41(1): 63–76. https://doi.org/10.4067/S0718-19572006000100009

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

Mercado-Santana JA; Santamaría-del-Ángel E; González-Silvera A; Sánchez-Velasco L; Gracia-Escobar MF; Millán-Núñez R and Torres-Navarrete C 2017. Productivity in the Gulf of California large marine ecosystem. *Environmental Development*, 22: 18–29. https://doi.org/10.1016/j.envdev.2017.01.003

Merrifield MA and Winant CD 1989. Shelf circulation in the Gulf of California: a description of the variability. *Journal of Geophysical Research*, 94(C12): 18133–18160. https://doi.org/10.1029/jc094ic12p18133

Munguia-Vega A; Green AL; Suarez-Castillo AN; Espinosa-Romero MJ; Aburto-Oropeza O; Cisneros-Montemayor AM; Cruz-Piñón G; Danemann G; Giron-Nava A; Gonzalez-Cuellar O; Lasch C; del Mar Mancha-Cisneros M; Marinone SG; Moreno-Báez M; Morzaria-Luna HN; Reyes-Bonilla H; Torre J; Turk-Boyer P; Walther M and Weaver AH 2018. Ecological guidelines for designing networks of marine reserves in the unique biophysical environment of the Gulf of California. *Reviews in Fish Biology and Fisheries*, 28(4): 749–776. https://doi.org/10.1007/s11160-018-9529-y

NOAA [National Oceanic and Atmospheric Administration] 2023. El Niño Southern Oscillation (ENSO)-Top 24 strongest El Niño and La Niña evento years by season. Available at https://psl.noaa.gov/enso/climaterisks/years/top24enso.html. Accessed on 18 may 2023.

Páez-Osuna F; Sánchez-Cabeza JA; Ruiz-Fernández AC; Alonso-Rodríguez AC; Piñón-Gimate A; Cardoso-Mohedano JG; Flores-Verdugo FJ; Carballo-Cenizo JL; Cisneros-Mata MA and Álvarez-Borrego S 2016. Environmental status of the Gulf of California: A review of responses to climate change and climate variability. *Earth Science Reviews*, 162: 253–268. https://doi.org/10.1016/j.earscirev.2016.09.015

Palomares García JR 1996. Estructura espacial y variación estacional de los copépodos en la Ensenada de La Paz. *Oceanides*, 11(1): 29-43.

Palomares-García JR; Suárez-Morales E and Hernández-Trujillo S 1998. Catálogo de los copépodos (Crustacea) pelágicos del Pacífico Mexicano. México, CICIMAR/ECOSUR, 352p.

Palomares-García JR; Gómez-Gutiérrez J and Robinson CJ 2013. Winter and summer vertical distribution of epipelagic copepods in the Gulf of California. *Journal of Plankton Research*, 35(5): 1009–1026. https://doi.org/10.1093/plankt/fbt052.

Palomares-García JR; Hernández-Trujillo S; Esqueda-Escárcega GM and Pérez-Morales A 2018. La biodiversidad de copépodos en la bahía de La Paz, Golfo de California. p. 171–188. In: Pérez-Morales A and Álvarez-García MC (Eds.), Estudios recientes en el Océano Pacífico Mexicano. México, Universidad de Colima.

Portela E; Beier E; Barton ED; Castro R; Godínez V; Palacios-Hernández E; Fiedler PC; Sánchez-Velasco L and Trasviña A 2016. Water masses and circulation in the tropical Pacific off central Mexico and surrounding areas. *Journal of Physical Oceanography*, 46(10): 3069–3081. https://doi.org/10.1175/jpo-d-16-0068.1

Quiroz-Martínez B; Salas-de-León DA; Gil-Zurita A; Monreal-Gómez MA; Coria-Monter E and Durán-Campos E 2023. Latitudinal and archipelago effect on the composition, distribution, and abundance of zooplanktonic organisms in the Gulf of California. *Oceanologia*, 65: 371–385. https://doi.org/10.1016/j.oceano.2022.11.001.

Razouls C; Desreumaux N; Kouwenberg J and de Bovée F 2005-2023. Biodiversity of Marine Planktonic Copepods (morphology, geographical distribution and biological data). Sorbonne University, CNRS. Available at http://copepodes.obs-banyuls.fr/en. Accessed on 21 September, 2023.

Robles-Tamayo CM; García-Morales R; Valdez-Holguín JE; Figueroa-Preciado G; Herrera-Cervantes H; López-Martínez J and Enríquez-Ocaña LF 2020. Chlorophyll *a* concentration distribution on the mainland coast of the Gulf of California, Mexico. *Remote Sensing*, 12(8): e-1335. https://doi.org/10.3390/rs12081335

Rocha-Díaz FA; Monreal-Gómez MA; Coria-Monter E; Salas-de-León DA; Durán-Campos E and Merino-Ibarra M 2021. Copepod abundance distribution in relation to a cyclonic eddy in a coastal environment in the southern Gulf of California. *Continental Shelf Research*, 222: 104436. https://doi.org/10.1016/j.csr.2021.104436

Rombouts I; Beaugrand G; Ibanez F; Gasparini S; Chiba S and Legendre L 2009. Global latitudinal variations in marine copepod diversity and environmental factors. *Proceedings: Biological Sciences*, 276(1670): 3053–3062. https://doi.org/10.1098/rspb.2009.0742

Santamaria-del-Angel E and Alvarez-Borrego S 1994. Gulf of California biogeographic regions based on coastal zone color scanner imagery. *Journal of Geophysical Research*, 99(C4): 7411–7421. https://doi.org/10.1029/93JC02154

Santamaria-del-Angel E; Alvarez-Borrego S and Müller-Karger FE 1994. The 1982-1984 El Niño in the Gulf of California as seen in coastal zone color scanner imagery. *Journal of Geophysical Research*, 99(C4): 7423–7431. https://doi.org/10.1029/93JC02147.

Schnack-Schiel SB; Niehoff B; Hagen W; Bottger-Schnack R; Cornils A; Dowidar MM; Pasternak A; Stambler N; Stubing D and Richter C 2008. Population dynamics and life strategies of *Rhincalanus nasutus* (Copepoda) at the onset of the spring bloom in the Gulf of Aqaba (Red Sea). *Journal of Plankton Research*, 30(6): 655–672. https://doi.org/10.1093/plankt/fbn029

Sew G and Todd P 2020. Effects of salinity and suspended solids on tropical phytoplankton mesocosm communities. *Tropical Conservation Science*, 13: 194008292093976. https://doi.org/10.1177/1940082920939760

Spinelli ML; Conçalves RJ; Villafañe VE and Capitanio FL 2016. Diversity of copepods in Atlantic Patagonian coastal waters throughout an annual cycle. *Ciencias Marinas*, 42(1): 31–47. https://doi.org/10.7773/cm.v42i1.2585

Stevens EM and Campbell CE 2022. Indication of possible shifts in copepod species composition in St. Pauls Inlet, a fjordal estuary connected to the Gulf of St. Lawrence. *Diversity*, 14(1): 59. https://doi.org/10.3390/d14010059

Storlazzi CD and Griggs GB 1998. Influence of El Niño-Southern Oscillation (ENSO) events on the Coastline of Central California. *Journal of Coastal Research*, 26: 146–153.

Suárez-Morales E 1989. Distribución, abundancia y nuevos registros de Corycaeidae (Copepoda: Cyclopoida) en el Banco de Campeche y Mar Caribe mexicano. *Boletín del Instituto Oceanográfico de Venezuela, Universidad de Oriente*, 28(1-2): 3–7.

Suárez-Morales E and Gasca R 1998. Updated checklist of the free-living marine Copepoda (Crustacea) of Mexico. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 69(1): 105–119.

Suárez-Morales E and Palomares-García R 1999. *Cymbasoma californiense*, a new monstrilloid (Crustacea: Copepoda: Monstrilloida) from Baja California, Mexico. *Proceedings of the Biological Society of Washington*, 112(1): 189–198.

Suárez-Morales E; Gutiérrez-Aguirre M; Gómez S; Perbiche-Neves G; Previatelli D; dos Santos-Silva EN; da Rocha CEF; Mercado-Salas N; Marques TM; Cruz-Auintanam Y and Satana-Piñeros AM 2020. Class Copepoda. p. 663–796. In: Damborenea C; Rogers DC; Thorp JH. (Eds.), Keys to Neotropical and Antartic Fauna. Thorp and Covich's Freshwater Invertebrates, Fourth Edition, Volume 5. London, Academic Press.

Thompson GA; Dinofrio EO and Alder VA 2013. Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer. *Journal of Plankton Research*, 35(3): 610–629. https://doi.org/10.1093/plankt/fbt014

Turner JT; Tester PA and Conley WJ 1984. Zooplankton feeding ecology: Predation by the marine cyclopoid copepod *Corycaeus amazonicus* F. Dahl upon natural prey. *Journal of Experimental Marine Biology and Ecology*, 84(2): 191–202. https://doi.org/10.1016/0022-0981(84)90212-0

Ulate K; Sánchez C; Sánchez-Rodríguez A; Alonso D; Aburto-Oropeza O and Huato-Soberanis L 2016. Latitudinal regionalization of epibenthic macroinvertebrate communities on rocky reefs in the Gulf of California. *Marine Biology Research*, 12(4): 389–401. https://doi.org/10.1080/17451000.2016.1143105

Urias-Leyva H; Aceves G; Avendano R; Saldierna R; Gómez J and Robinson C 2018. Regionalization in the distribution of larval fish assemblages during winter and autumn in the Gulf of California. *Latin American Journal of Aquatic Research*, 46(1): 20–36. https://doi.org/10.3856/vol46-issue1-fulltext-4

Valdés L; López-Urrutia A; Beaugrand G; Harris PG and Irigoien X 2022. Seasonality and interannual variability of copepods in the Western English Channel, Celtic Sea, Bay of Biscay, and Cantabrian Sea with a special emphasis to *Calanus helgolandicus* and *Acartia clausi*. *Journal of Marine Science*, 79(3): 727–740. https://doi.org/10.1093/icesjms/fsac052

Valdéz-Holguín JE and Lara-Lara R 1987. Primary productivity in the Gulf of California effects of El Niño 1982-1983 event. *Ciencias Marinas* 13(2): 34–50. https://doi.org/10.7773/cm.v13i2.533

Walter TC and Boxshall G 2023. World of Copepods Database. Available at https://www.marinespecies.org/copepoda on 2022-06-16. Accessed on 23 January 2023. https://doi.org/10.14284/356

Wiebe PH; Copley N; Van Dover C; Tamse A and Manriquez F 1988. Deep water zooplankton of the Guaymas Basin hydrothermal vent field. *Deep-Sea Research*, 35(6): 985–1013. https://doi.org/10.1016/0198-0149(88)90072-6

Wolfenden RN 1905. Plankton Studies: preliminary notes upon new or interesting species. Part 1. Copepoda. London and New York, Rebman Limited, 24p.

Wyeth AC; Grünbaum D and Keister JE 2022. Effects of hypoxia and acidification on *Calanus pacificus*: behavioral changes in response to stressful environments. *Marine Ecology Progress Series*, 697: 15–29. https://doi.org/10.3354/meps14142

Wyrtki K 1965. The annual and semiannual variation of sea surface temperature in the North Pacific Ocean. *Limnology and Oceanography*, 10: 307. https://doi.org/10.4319/lo.1965.10.3.0307

Zeitzschel B 1969. Primary productivity in the Gulf of California. *Marine Biology*, 3(3): 201–207. https://doi.org/10.1007/bf00360952

ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

Conceptualization and design, analysis and interpretation of the data, preparation of figures and writing: VOK. Performed research, acquisition of data, critical review and editing: MEH.

Consent for publication

All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

Competing interests

The authors declare no competing interest.

Data availability

All study data are included in the article and supplementary material.

Funding and grant disclosures

Shiptime aboard the R/V "El Puma" for the CORTES 2 and 3 cruises was provided by the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico. Sampling and study of the material collected during the CORTES 2 and 3 cruises were supported by the CONACYT (Mexico) grant ICECXNA-021926. The authors thank all members of the technical and scientific crews for their help during the sampling operations aboard the R/V "El Puma".

Study association

This study is part of the Doctoral Dissertation of VOK in the Posgrado en Ciencias del Mar y Limnología, at the Unidad Academica Mazatlán, Universidad Nacional Autónoma de México.

Study permits

There were not required permissions to collect, or violation of any law either, because of the year of the sampling.

APPENDIX

Table A1. Species list of copepods collected in the Gulf of California during the CORTES cruises in 1985. The abbreviated names are used in the CCA analyses. The species occurrence in each cruise is indicated with an "x" (CORTES 2 and 3 columns).

Order	Species	Abbreviated name	CORTES 2	CORTES 3
Calanoida	**Acartidae**			
	Acartia (Odontacartia) lilljeborgii Giesbrecht, 1889	*Acalil*	×	×
	Acartia (Acanthartia) tonsa Dana, 1849	*Acaton*	×	×
	Aetideidae			
	Aetideus armatus (Boeck, 1872)	*Aetarm*	×	×
	Euchirella bitumida With, 1915	*Eucbi*	×	×
	Euchirella rostrata (Claus, 1866)	*Eucro*	×	×
	Euchirella sp.	*Eucsp*		×
	Augaptilidae			
	Augaptilus megalurus Giesbrecht, 1889	*Augmeg*	×	×
	Euaugaptilus filigerus (Claus, 1863)	*Euafil*	×	
	Haloptilus ornatus (Giesbrecht, 1893)	*Halor*	×	×
	Calanidae			
	Calanus pacificus Brodsky, 1948	*Calpac*	×	×
	Cosmocalanus darwinii (Lubbock, 1860)	*Cosdar*	×	
	Nannocalanus minor (Claus, 1863)	*Nanmin*	×	×
	Undinula vulgaris (Dana, 1849)	*Undvul*	×	×
	Candacidae			
	Candacia curta (Dana, 1849)	*Cancur*	×	×
	Candacia simplex (Giesbrecht, 1889)	*Cansim*	×	×
	Centropagidae			
	Centropages furcatus (Dana, 1849)	*Cenfur*	×	×
	Clausocalanidae			
	Clausocalanus furcatus (Brady, 1883)	*Clafur*		×
	Clausocalanus jobei Frost & Fleminger, 1968	*Clajob*	×	×
	Eucalanidae			
	Eucalanus californicus Jhonson M.W., 1938	*Euccal*	×	×
	Eucalanus elongatus elongatus (Dana, 1848)	*Eucelo*	×	
	Eucalanus hyalinus (Claus, 1866)	*Euchya*	×	×
	Pareucalanus sewelli (Fleminger, 1973)	*Parsew*	×	×
	Rhincalanus nasutus Giesbrecht, 1888	*Rhinas*	×	×
	Subeucalanus subcrassus (Giesbrecht, 1888)	*Subsub*	×	×
	Subeucalanus subtenuis (Giesbrecht, 1888)	*Subsub*	×	×
	Euchaetidae			
	Euchaeta marina (Prestandrea, 1833)	*Eucmar*	×	×
	Euchaeta plana Mori, 1937	*Eucpla*		×
	Heterorhabdidae			
	Heterorhabdus papilliger (Claus, 1863)	*Hetpap*	×	×
	Heterorhabdus sp.	*Hetsp*	×	
	Lucicutiidae			
	Lucicutia flavicornis (Claus, 1863)	*Lucfla*	×	×
	Lucicutia pacifica Brodsky, 1950	*Lucpac*	×	×
	Metridinidae			
	Metridia brevicauda Giesbrecht, 1889	*Metbre*	×	
	Pleuromamma abdominalis abdominalis (Lubbock, 1856)	*Pleabd*	×	×

Table A1. Cont.

Order	Species	Abbreviated name	CORTES 2	CORTES 3
	Pleuromamma borealis Dahl F., 1893	*Plebor*	×	×
	Pleuromamma gracilis gracilis Claus, 1863	*Plegra*	×	×
	Paracalanidae			
	Paracalanus aculeatus Giesbrecht, 1888	*Paracu*		×
	Paracalanus parvus parvus (Claus, 1863)	*Parpar*	×	
	Phaennidae			
	Phaenna spinifera Claus, 1863	*Phaspi*	×	×
	Pontellidae			
	Labidocera acuta (Dana, 1849)	*Labacu*	×	×
	Labidocera acutifrons (Dana, 1849)	*Labacu*	×	×
	Labidocera jollae Esterly, 1906	*Labjol*	×	
	Labidocera trispinosa Esterly, 1905	*Labtri*		×
	Pontella agassizi Giesbrecht, 1895	*Ponaga*		×
	Pontella danae Giesbrecht, 1889	*Pondan*		×
	Pontellina plumata (Dana, 1849)	*Ponplu*		×
	Pontellopsis armata (Giesbrecht, 1889)	*Ponarm*		×
	Pontellopsis occidentalis Esterly, 1906	*Ponocc*	×	×
	Pontellopsis regalis (Dana, 1859)	*Ponreg*		×
	Pontellopsis yamadae Mori, 1937	*Ponyam*		×
	Scolecithricidae			
	Scaphocalanus affinis (Sars G.O., 1905)	*Scaaff*	×	×
	Scolecithricella abyssalis Giesbrecht, 1888)	*Scoaby*	×	×
	Scolecithricella nicobarica (Sewell, 1929)	*Sconic*	×	×
	Scolecithrix bradyi Giesbrecht, 1888	*Scobra*		×
	Scolecithrix danae (Lubbock, 1856)	*Scodan*	×	×
	Temoridae			
	Temora discaudata Giesbrecht, 1889	*Temdis*	×	×
	Temoropia mayumbaensis Scott T., 1894	*Temmay*	×	×
Cyclopoida	**Clausidiidae**			
	Halicyclops sp.	*Halsp*	×	
	Corycaeidae			
	Onychocorycaeus catus (Dahl F., 1894)	*Onycat*	×	×
	Corycaeus crassiusculus, Dana 1849	*Corcra*	×	×
	Urocorycaeus lautus (Dana, 1849)	*Urolau*	×	
	Corycaeus speciosus Dana, 1849	*Corspe*	×	×
	Lubbockidae			
	Lubbockia squillimana Claus, 1863	*Lubsqu*	×	×
	Oithonidae			
	Oithona setigera setigera (Dana, 1849)	*Oitset*	×	×
	Oithona sp.	*Oitsp.*	×	
	Oncaeidae			
	Oncaea conifera Giesbrecht, 1891	*Onccon*	×	×
	Oncaea media Giesbrecht, 1891	*Oncmed*	×	×
	Oncaea venusta Philippi, 1843	*Oncven*	×	×
	Sapphirinidae			
	Copilia mirabilis Dana, 1852	*Copmir*	×	×
	Sapphirina darwinii Haeckel, 1864	*Sapdar*	×	×
	Sapphirina gastrica Giesbrecht, 1891	*Sapgas*	×	×
	Sapphirina gemma Danna 1852-1853	*Sapgem*	×	×

Table A1. Cont.

Order	Species	Abbreviated name	CORTES 2	CORTES 3
	Sapphirina metallina Dana, 1849	*Sapmet*	×	×
	Sapphirina opalina Dana, 1849	*Sapopa*	×	×
	Sapphirina stellata Brady, 1891	*Sapste*	×	
Harpacticoida	**Ectinosomatidae**			
	Microsetella rosea (Dana, 1847)	*Micros*	×	×
	Peltidiidae			
	Clytemnestra scutellata Dana, 1847	*Clyscu*	×	×
	Tachidiidae			
	Euterpina acutifrons (Dana, 1847)	*Eutacu*	×	
Siphonostomatoida	**Pontoeciellidae**			
	Pontoeciella abyssicola (Scott T., 1893)	*Ponaby*	×	×
	Rataniidae			
	Ratania flava Giesbrecht, 1893	*Ratfla*		×

Table A2. List of published research about copepods in the Gulf of California. The most comparable aspects are included: Reference (Ref.), period of study (Per. st.), zone of the gulf (Zone), sampling method (Samp.), number of stations (N° st.), maximum sampled depth (Max. dpt.), average abundance expressed in ind/10 m^3 (Avg. abu.), richness (or descriptions/new records) (Rich.) and the three most abundant species (Dom. spec.). The most comparable contributions to this work are highlighted in boldface. ND: not defined by the author or data not found. Please note that some of the presented data were not directly given by the authors and were calculated, so there could be some discrepancies.

Ref.	Per. st.	Zone	Samp.	N° st.	Max. dpt.	Avg. abu.	Rich.	Dom. spec.
Fleminger (1967)	apr 1956-sep 1963	NGC-SGC	Conical net (333 µm)	33	5	ND	2 spp. nov.	ND
Manrique (1977)	ND	ND	ND	ND	ND	ND	ND	*Calanus pacificus, Acartia tonsa, Acartia lilljeborgii*
Brinton et al. (1986)	ND	NGC-SGC	Literature revision	ND	ND	ND	132 spp.	ND
Jiménez-Pérez and Lara-Lara (1988)	**mar ‘83**	**CGC, SGC**	**Bongo nets (333 µm)**	**22**	**250 m**	**340,000**	**76 spp.**	***Pleuromamma gracilis, Eucalanus subtenuis, Eucalanus pileatus***
Wiebe et al. (1988)	jul-aug 1985	CGC	Opening-closing nets (333 µm)	1	1000 m	3705	67 spp.	*Gaidius minutus, Spinocalanus* sp., *Candacia magna*
Lavaniegos-Espejo and Lara-Lara (1990)	**mar-apr 1984**	**CGC-EGC**	**Bongo nets (333 µm)**	**26**	**200 m**	**560,000**	**ND**	**ND**
Palomares-García (1996)	1984	SGC (Bahía de la Paz)	Conical net (250 µm)	ND	Surface	ND	59 spp.	*Acartia clausii, Acartia lillljeborjii, Paracalanus parvus*
Lavaniegos-Espejo and López-Cortés (1997)	jan-nov 1994	SGC (Bahía de la Paz)	Conical net (333 µm)	1	30 m	672,000	20 spp.	*Acrocalanus longicornis, Centropages furcatus, Nannocalanus minor*
Suárez-Morales and Gasca (1998)	ND	Mexican Pacific and Atlantic	Literature revision	ND	ND	ND	154 spp.	ND
Lavaniegos-Espejo and González-Navarro (1999)	feb-aug 1990, may-nov 1992 and jan 1993	SGC	Bongo nets (300/500 µm)	1	60 m	62,077	93 spp.	*Temora discaudata, Nannocalanus minnor, Oithona plumata*
López-Cortés et al. (1999)	mar-apr 1995	CGC	ND	9	300 m	ND	3 spp.	*Calanus pacificus, Rhincalanus nasutus*
Suárez-Morales and Palomares-García (1999)	sep-96	SGC, Bahía de Madalena	Conical net (333 µm)	ND	ND	ND	1 sp. nov.	ND

Table A2. Cont.

Ref.	Per. st.	Zone	Samp.	N° st.	Max. dpt.	Avg. abu.	Rich.	Dom. spec.
Gómez (2000)	apr-jun 1991	SGC (Pabellones)	Plastic corer	15	Surface (2 cm)	ND	3 spp.;1 sp. nov.	ND
Gómez (2003)	1991 and 2001	EGC (Pabellones, Urias)	Plastic corer	2	Surface (10 cm)	ND	3 sp. nov.	ND
Lavaniegos-Espejo et al. (2012)	may 2003-oct 2004	SGC (Bahía de los Ángeles)	Conical net (200 μm)	4	Surface	ND	24 spp.	*Paracalanus parvus, Acartia tonsa, Acartia clausii*
Palomares-García et al. (2013)	**jan-aug 2007**	**NGC, CGC**	**Opening-closing conical nets (333 um)**	**34**	**200 m**	**100,000-500,000**	**52 spp.**	***Pleuromamma gracilis, Calanus pacificus, Rhincalanus nasutus***
Beltrán-Castro and Hernández-Trujillo (2016)	ND	ND	Conical net (300 μm)	ND	ND	ND	101 spp.	ND
Cruz-Hernández et al. (2018)	jul-aug 2011	CGC	Opening-closing conical net (505 μm)	21	200 m	46,647-72,471	57 spp.	*Nannocalanus minor, Scolecithrix danae, Temora discaudata*
Cruz-Hernández et al. (2019)	jun-jul 2010	EGC	Opening-closing conical net (505 μm)	17	200 m	62,161	78 spp.	*Nannocalanus minor, Rhincalanus nasutus, Subeucalanus subtenuis*
Gasca et al. (2015)	apr 2005 and mar 2015	CGC-SGC	Remotely operated submersible	ND	3000 m	ND	1 sp. (new record)	ND
Gómez (2018a)	aug 2000 and feb 2007	CGC, SGC	Sediment corer	ND	2120 m	ND	1 sp. nov.	ND
Gómez (2018b)	aug 2000	CGC	Sediment corer	30	2120 m	ND	2 spp. nov.	ND
Gómez (2018c)	feb-07	CGC	Sediment corer	26	1642 m	ND	2 spp. nov.	ND
Gómez-Gutiérrez and Hernández-Trujillo (1994)	aug 1988	EGC	Bongo nets (333/505 μm)	9	600 m	24,176.20	51 spp.	*Paracalanus parvus, Pleuromamma abdominalis, Euchaeta marrina*
Hernández-Nava and Álvarez-Borrego (2013)	sep-dec 2009	CGC	Conical net (150 μm)	12	Surface	10,000,000-50,000,000	24 spp.	*Acartia* sp., *Paracalanus* sp., *Oncaea* sp.
Gómez-Gutiérrez et al. (2014)	nov-10	EGC (Islas Marías)	Conical net (333 μm)	11	Surface	58,576.30	35 spp.	*Calanopia minor, Clausocalanus jobei, Acrocalanus gibber*
Palomares-García et al. (2018)	1980-2007	SGC (Bahía de la Paz)	Literature revision	39	400 m	1,000,000	146	*Temora discaudata, Centropages furcatus, Oithona plumata*
Beltrán-Castro et al. (2020)	jan 2014-dec 2015	EGC (Cabo Pulmo)	Conical net (300 μm)	81	5 m	242,243	49 spp.	*Oncaea venusta, Paracalanus parvus, Clausocalanus jobei*
Coria-Monter et al. (2020)	sep 2008-aug 2009	SGC (Bahía de la Paz)	Bongo nets (333 μm)	56	200 m	39,000-75,520	ND	ND
Rocha-Díaz et al. (2021)	feb-07	SGC	Bongo nets (333 μm)	13	200 m	1,480-15,020	ND	ND
Quiroz-Martínez et al. (2022)	mar-apr 1978	GC	Bongo nets (202 μm)	41	95 m	32,000-90,000	ND	ND
Gómez and Yanez-Rivera (2023)	aug 2000 and aug 2012	SGC	Multiple sediment corer	ND	2120 m	ND	1 sp. nov.	ND

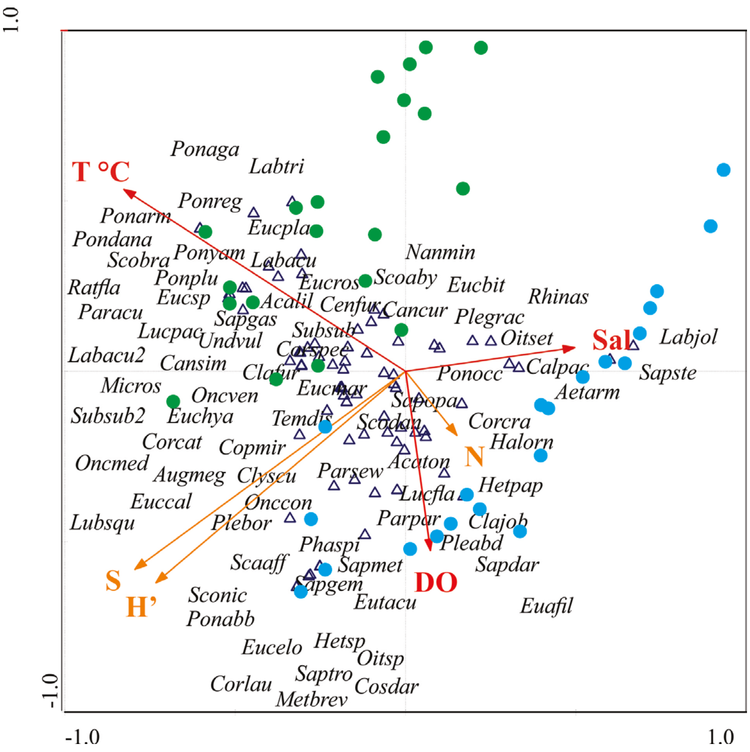

Figure S1. Influence of the environmental variables (red vectors; T°-temperature, Sal-salinity, DO-dissolved oxygen) over the ecological indices (orange vectors; S-richness, H’- diversity, N-abundance) and the species composition (blue triangles) registered in the Gulf of California, in 1985. The CCA includes the stations of the cold (blue circles) and the warm (green circles) seasons. Results correspond to the environmental variables measured at a depth of 20 m.

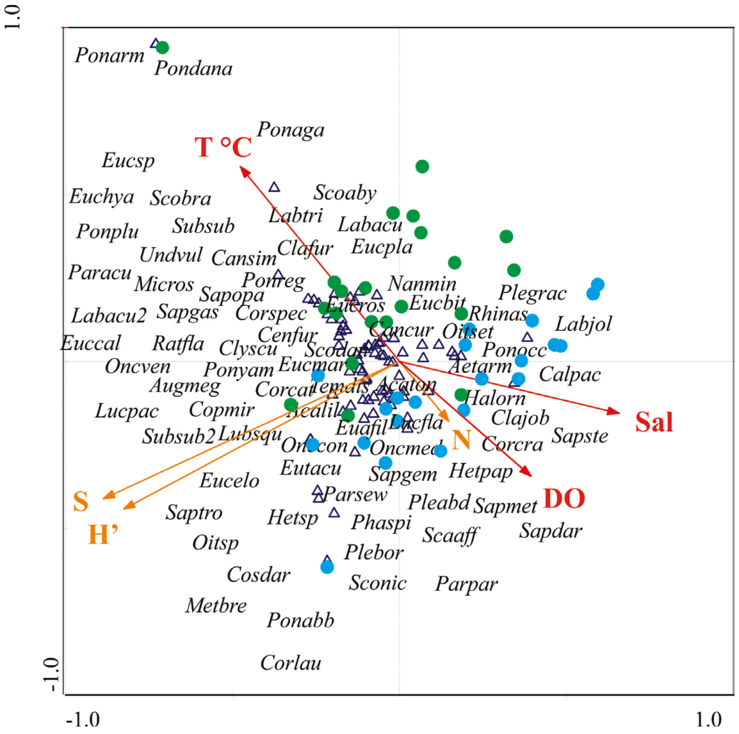

Figure S2. Influence of the environmental variables (red vectors; T°-temperature, Sal-salinity, DO-dissolved oxygen) over the ecological indices (orange vectors; S-richness, H’-diversity, N-abundance) and the species composition (blue triangles) registered in the Gulf of California, in 1985. The CCA includes the stations of the cold (blue circles) and the warm (green circles) seasons. Results correspond to the environmental variables measured at a depth of 75 m.