



# Abundance and diversity patterns and environmental drivers of Peracarida (Arthropoda, Crustacea) macrofauna from the deep sea of the southwestern Gulf of Mexico

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## ABSTRACT

We present unique data of abundance, spatial diversity, and bathymetric patterns of the Peracarida communities of the economic and ecological important scarce studied area of the southern Gulf of Mexico. Peracarida macrofauna was collected from 63 sites in a large geographical area (92.67°–96.70° W, 18.74°–23.04° N) with a wide bathymetric gradient (185–3740 m depth) of the deep-sea southwestern Gulf of Mexico. The samples were obtained onboard the R/V Justo Sierra (Universidad Nacional Autónoma de México, UNAM) using a Reineck-type box corer during four oceanographic cruises (SOGOM 1–4; 2015–2018). We examined the bathymetric and spatial patterns of standardized abundance (ind. m<sup>-2</sup>) and taxonomic diversity (Hill numbers,  $q = 0, 1, \text{ and } 2$ ). Abundance patterns were related to environmental parameters (organic matter, aromatic and aliphatic hydrocarbons, bottom water temperature, dissolved oxygen and grain composition). We collected 684 specimens belonging to 53 Peracarida families of 4 orders (Amphipoda, 19; Isopoda, 17; Tanaidacea, 13; and Cumacea, 4). The most abundant orders were Amphipoda and Tanaidacea, representing 36.4% and 35.8% of the total abundance, respectively, followed by Isopoda (25.1%). Cumacea was the least abundant order (2.7%). The top ten abundant families in order were Apseudidae, Phoxocephalidae, Caprellidae, Desmosomatidae, Nototanaidae, Nannoniscidae, Tanaellidae, Ischnomesidae, Podoceridae, and Agathotanaididae, accounting for 66% of the total relative abundance. The abundance decreased with increasing depth. Highest values were recorded in the northwestern region of the study area and in the Campeche Bay salt domes zone, whereas the lowest abundance values were registered at the abyssal locations and in some sites located in the Coatzacoalcos and Campeche Canyons. The composition and structure of the peracarid community showed shifts related to depth. The major structural abiotic factors of the Peracarida community were: latitude, depth, temperature, and sediment aliphatic hydrocarbons. The diversity based on the three estimated Hill numbers consistently decreased with increasing depth. We recorded intermediate and low diversity values in almost the entire study area, except for the Campeche Bay salt domes zone and northwestern region, where intermediate and high diversity values were registered.

## 1. Introduction

The Challenger Expedition, conducted between 1872 and 1876, marked the beginning of global deep-sea exploration (McIntosh, 1885). The efforts of these pioneers were followed by important expeditions

such as those to Talisman (France), Albatross (E. U.), and Galathea (Denmark) (Gage and Tyler, 1991). With the recent increase in efforts, regional-level efforts are underway (e.g., Brandt et al., 2007b, 2018; Wilson, 2017). These investigations tended to focus on the dominant taxonomic groups. Within the macrofauna communities (composed of

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metazoans with a length of <1.5 cm that could be retained in a sieve of mesh size 250–500  $\mu\text{m}$  (Gage, 2001; Rex et al., 2006; Taylor et al., 2017)), polychaetes, mollusks, and peracarids are the dominant taxa and represent up to 80% of the total abundance (Grassle and Maciolek, 1992). Peracarids are usually recorded as the second most abundant taxon in the macrofauna (Gage, 2001; Rex et al., 2006) despite being recorded as the dominant group in some studies (Almeida et al., 2017; Brandt et al., 2019; Brandt et al., 2018). This difference could typically be a consequence of the device used to collect the biological samples; however, Peracarida is undoubtedly a major macrofaunal component.

Amphipods, isopods, and tanaidaceans are the most abundant and diverse orders of Peracarida (Jamieson, 2015). Amphipods are one of the primary bioturbator fauna (Brandt et al., 2023), and tens of thousands have been reported in traps in the hadal zone (Blankenship et al., 2006). Tanaidaceans are among the most diverse and abundant macrofaunal groups in the deep sea (Larsen, 2005; Wilson, 1987). They are predatory carnivores, detritivores, burrowers, and suspensivores; however, many are probably opportunistic (Larsen, 2005) and contribute to the rapid utilization of organic matter from sporadic inputs to the deep sea (Gooday, 1990). In addition, the importance of tanaidaceans as bioindicators of bathymetric zones has been highlighted (Hernández-Robles and Escobar-Briones, 2008). Isopods are also among the most diverse and abundant Peracarida orders (Brandt et al., 2007a; Wilson, 1987) with the suborder Asellota being the most diverse and species-rich group inhabiting the deep sea (Brandt et al., 2007a; Hartebrødt, 2020; Poore and Wilson, 1993; Wilson, 2008). Isopods exhibit diverse feeding habits. They could be scavengers, predators, parasites, detritus feeders, or filter feeders and are herbivores, carnivores, or omnivores (Hartebrødt, 2020). They participate in bioturbation and bioirrigation sediment processes to oxygenate subsurface layers and intervene in organic matter burial (Crawshaw et al., 2019), thereby promoting bacterial activity and facilitating organic carbon remineralization (Parkes et al., 1994; Snelgrove, 1998; Zhang et al., 2010). Peracarids are also involved in the transport, burial, and metabolism of pollutants (Banta and Andersen, 2003; Snelgrove, 1998). They remove pollutants from the water column that pass through the food chain to other parts of the system (Gage, 2001; Snelgrove, 1998). Additionally, they affect sediment transport by increasing the susceptibility of the system to erosion (Grant et al., 1982). Moreover, owing to their active participation in global biogeochemical cycles through nutrient recycling, ecological interactions, and the physical transformation of the inhabiting environment, Peracarida constitutes a fundamental component of deep-sea benthic macrofauna communities.

The abundance and diversity patterns of peracarids have been examined globally (Błażewicz et al., 2019; Brandt et al., 2007a; Brandt, 2001; Brandt et al., 1997; Brandt et al., 2005; Brandt et al., 1997; Brökeland et al., 2007; Di Franco et al., 2021; Frutos and Jazdzewska, 2019; Gage, 2004; Golovan et al., 2013; Rehm et al., 2007) and specifically in the northern region of the GoM (Larsen, 2005; Larsen, 2003; Wilson, 2008). The most abundant order identified in these studies varied depending on the region and particularly with the sampling device used (Almeida et al., 2017; Larsen, 2005). In addition, the widely distributed, abundant, and diverse groups in the deep-sea, such as the isopods of the suborder Asellota (Brandt et al., 2007a; Wilson, 2008) and the subfamily Apsseudinae of the tanaidaceans (Larsen, 2005), have been highlighted. Most of the studies on deep-sea peracarids in the Mexican deep waters of the GoM were related to taxonomic characteristics (Escobar-Briones and Winfield, 2003; Ortiz et al., 2022; Ortiz et al., 2019; Ortiz et al., 2018; Paz-Rios and Pech, 2021; Winfield et al., 2016; Winfield et al., 2006); consequently, those dealing with ecological traits are scarce (e.g., Hernández-Ávila et al., 2021). The social, economic, and ecological importance of the GoM highlights the need for sound knowledge of this large ecosystem that could help to understand its resilience to stressors. In addition, the GoM is subjected to chronic and eventual contamination sources, such as large oil spills (Ixtoc 1, 1979–1980; Deepwater Horizon, 2010) that affect the ecosystem

(Murawski et al., 2020; Pulster et al., 2020; Reuscher et al., 2020; Schwing et al., 2020). This study was designed to contribute to the knowledge of Peracarida macrofauna communities by (i) evaluating the taxonomic composition of Peracarida macrofauna communities at the family level and (ii) analyzing their spatial distribution patterns in the deep sea of the southwestern GoM.

## 2. Materials and methods

### 2.1. Study area

The Gulf of Mexico is a semi-closed basin located in a transitional zone between tropical and subtropical climates (between 18° and 30° N and 82° and 98° W) that communicates with the Caribbean Sea and Atlantic Ocean through the Yucatan Channel and Strait of Florida, respectively (Monreal-Gómez et al., 2004). The sea is surrounded by three countries (Cuba, USA, and Mexico) and is one of the most productive and economically important ecosystems on the planet (Kumpf et al., 1999) primarily because of the hydrocarbon extraction and fishery resources. It has an area of approximately 1,540,000 km<sup>2</sup> (Ward and Tunnell, 2017), of which, more than half (55%) is in the Mexican Economic Exclusive Zone. Most of its waters (65%) are deep, 42% correspond to continental slope (200–3000 m), and 24% correspond to abyssal plains (> 3000 m) (Ward and Tunnell, 2017). The maximum depth is approximately 4000 m on the SIGSBEE Plain (Darnell, 2015). A highly homogeneous mass of water, with a salinity close to 35 PSU, temperature of approximately 4.3 °C, and dissolved oxygen values higher than those recorded in shallower waters, is present at a depth of 1500 m. The listed characteristics are highly similar to those of North Atlantic Deep Water (NADW). The deep Gulf bottoms are mainly composed of terrigenous and biogenic mud. A general net current flows in a west–north–east direction around the Gulf from the Campeche Bank to Florida (Monreal-Gómez et al., 2004) and is mainly affected by the Loop Current. The current enters through the Yucatán Channel, leaves through the Florida Straits, and produces several cyclonic-anticyclonic gyres of different scales depending on wind and pressure effects (Monreal-Gómez and Salas-de-León, 1997). The principal freshwater discharges into the GoM originate from the Mississippi River in the north and the Grijalva–Usumacinta River system in the south.

### 2.2. Sampling and sample processing

Sediment samples were collected onboard the R/V Justo Sierra of the Universidad Nacional Autónoma de México (UNAM) in the southwestern GoM during the oceanographic cruises of SOGOM 1 to 4 conducted from June 3 to 27, 2015; August 31 to September 20, 2016; April 21 to May 15, 2017; and August 29 to September 20, 2018. The sampling sites were located within a geographic range of 92.67°–96.70° west longitude and 18.74°–23.04° north latitude, at a depth range of 185–3740 m (Fig. 1). Although the sampling design considered 63 locations on each cruise, only 60, 62, 56, and 62 were successfully sampled from SOGOM 1 to SOGOM 4, respectively, for logistic reasons. The original numbering of each site was retained for cross-cruise comparison.

Four environmental variables were measured in situ. Depth (m) was recorded using the ship's echo sounder. Dissolved oxygen (mL L<sup>-1</sup>), salinity (PSU), and temperature (°C) of bottom water were measured with a CTD probe (Model Sea-Bird SBE 9 plus). For safety, the device was placed 16–932 m (average 217 m) from the bottom, depending on the depth. Latitude and longitude were recorded when the corer reached the seabed. The percentages of sand, silt, and clay in the sediment were measured using a Beckman Coulter model LS 230 laser diffraction analyzer (Small Volume Modulo Plus). Details of the organic matter and carbonate content measurements have been described by Quintanar-Retama et al. (2022). Details of the aliphatic and aromatic hydrocarbon concentration measurements have been described by Quintanar-Retama

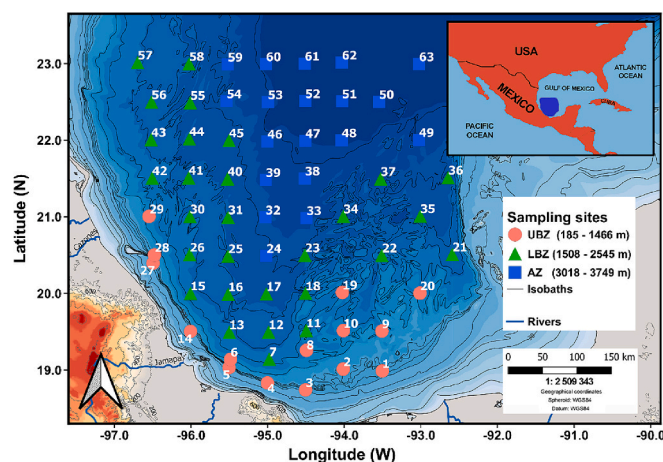


Fig. 1. Location of the 63 sampling sites from the oceanographic cruises SOGOM 1–4 Upper bathyal zone (UBZ, pink circle); lower bathyal zone (LBZ, green triangle), and abyssal zone (AZ, blue square). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al. (2023).

Sediment was collected using a Reineck-type box corer with 0.16 m<sup>2</sup> effective area. A sediment sample of surface area 0.08 m<sup>2</sup> from a depth of 13 cm was collected for faunal analysis in each core. Faunal samples were sieved onboard with filtered seawater using a mesh of 500 µm. Taxonomic identification was performed based on general taxonomic literature (e.g., Kensley and Schotte, 1989; Wetzler and Brusca, 1997; LeCroy et al., 2000; LeCroy, 2002, 2004; Larsen, 2005). Only known fauna were included in the analysis, and the taxonomic names were cross-checked using the data from World Register of Marine Species (WoRMS, [www.marinespecies.org](http://www.marinespecies.org)). Further details of the sampling process can be found in Armenteros et al. (2022) and; Quintanar-Retama et al. (2023, 2022).

### 2.3. Data analysis

We developed a standardized abundance matrix identifying the fauna at the family level, totaling the organisms recorded at each site during the four cruises, and standardized them as ind. m<sup>-2</sup>. For the environmental analysis, the average of the values obtained at each site was calculated. The sampling sites were organized into three depth categories (DCs): the upper bathyal zone (UBZ) (185–1500 m), lower bathyal zone (LBZ) (1501–3000 m), and abyssal zone (AZ) (3001–3740 m). The limit between the bathyal and abyssal regions at 3000 m was based on literature (e.g., Watling et al., 2013; Harris, 2020) and GoM bathymetry.

Sand percentage was not considered in the analysis because the highest value was merely 2.2% (site 27), whereas it was <1% in 82% of the sampled sites (52 sites). We also performed Pearson correlation analysis of the environmental variables using the stats package in R (R Core Team, 2022) to determine which variables correlated. Clay and salinity were not considered in the analysis of environmental factors because of their high correlations ( $\rho > 0.9$ ) with silt and temperature, respectively. To reduce the dimensionality and assess the environmental characteristics of each depth category, principal component analysis was performed using the normalized matrix of environmental variables after covariable removal. This was elaborated using the vegan package in R (Oksanen et al., 2022); the pheatmap and factoextra libraries were used for the visualization of results (Kolde, 2019).

Box plots were constructed based on the standardized abundance matrix to assess possible variations in abundance based on the depth. In addition, we performed a Kruskal–Wallis test to evaluate the significance of the differences in abundance among the depth zones. We also

constructed percentage and basic stacked bar charts to analyze site-specific bathymetric changes in the standardized and relative abundance measures. These analyses were performed using the ggplot2 package (Wickham, 2016) in R. The significance of the relationship between the depth and abundance was evaluated using Spearman's correlation.

The standardized abundance matrix was square-root transformed to avoid outlier bias. Subsequently, a pairwise similarity matrix of the sites was generated based on the Bray–Curtis index (Clarke et al., 2014), and a non-metric multidimensional scaling (nMDS) was performed (Oksanen et al., 2022; Wickham, 2016) using the vegan and ggplot2 packages in R. Additionally, an Analysis of Similarities (ANOSIM) (999 permutations, Bray–Curtis distance) was performed to test the differences among DCs using the vegan package in R (Oksanen et al., 2022).

Spearman correlation coefficients (RS) between biotic and abiotic similarity matrices were calculated using the BIOENV routine (Clarke et al., 2008) and the vegan package (Oksanen et al., 2022). Nine environmental factors (latitude, longitude, depth, temperature, dissolved oxygen, polycyclic aromatic hydrocarbons, aliphatic hydrocarbons, organic matter, and silt) were considered for the analysis. The abiotic factor similarity matrix was generated based on Euclidean distance from the normalized matrix of environmental variables.

Based on the abundance data matrix, we computed the diversity estimates (Hill numbers,  $q = 0, 1, \text{ and } 2$ ) using the iNEXT package (Chao et al., 2014) in R. Hill numbers include the three commonly used diversity measures: species richness ( $q = 0$ ), Shannon diversity ( $q = 1$ ), and Simpson diversity ( $q = 2$ ). We also constructed continuous extrapolation and rarefaction sampling curves for the three Hill numbers.

The spatial abundance distribution map was constructed with standardized abundance values, whereas the spatial diversity distribution map was prepared with the estimated values of taxonomic richness ( $q = 0$ ) at a 0.6 sampling coverage. All maps were created using QGIS 3.12 software. The sites were aggregated into classes using the natural breakage methodology (Jenks) (Smith et al., 2015).

## 3. Results

### 3.1. Environmental analysis

Principal component analysis showed that latitude, organic matter, polycyclic aromatic hydrocarbons, and carbonate concentrations in sediments were the environmental variables most related to component one, whereas longitude and aliphatic hydrocarbon content in sediments were the factors most related to component two. Both the components accounted for 70% of the observed variability. In addition, the sites were ordered in a bathymetric gradient in which the abyssal region localities were characterized by high latitude, bottom water DO, and carbonate content in the sediment. Localities in the upper bathyal region were characterized by high bottom water temperature and high content of aromatic hydrocarbons, organic matter, and silt (Figs. 2, 3, and 4). Further details of the patterns observed in the measured environmental variables can be found in Armenteros et al. (2022) and Quintanar-Retama et al. (2023, 2022).

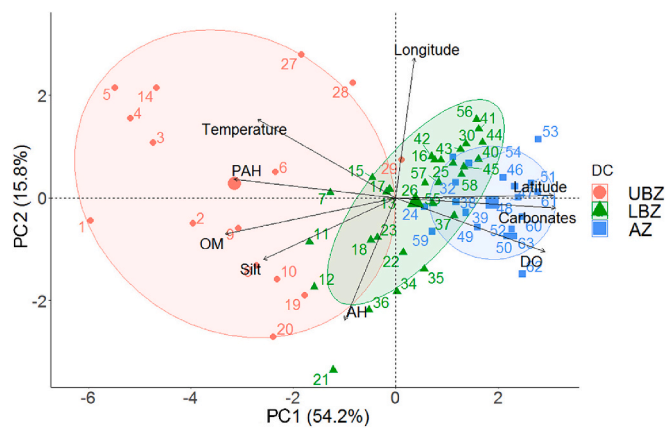
Abbreviations: Polycyclic aromatic hydrocarbons (PAH); organic matter (OM); aliphatic hydrocarbons (AH); dissolved oxygen (DO); depth category (DC); upper bathyal zone (UBZ); lower bathyal zone (LBZ); and abyssal zone (AZ)

### 3.2. Description of the fauna

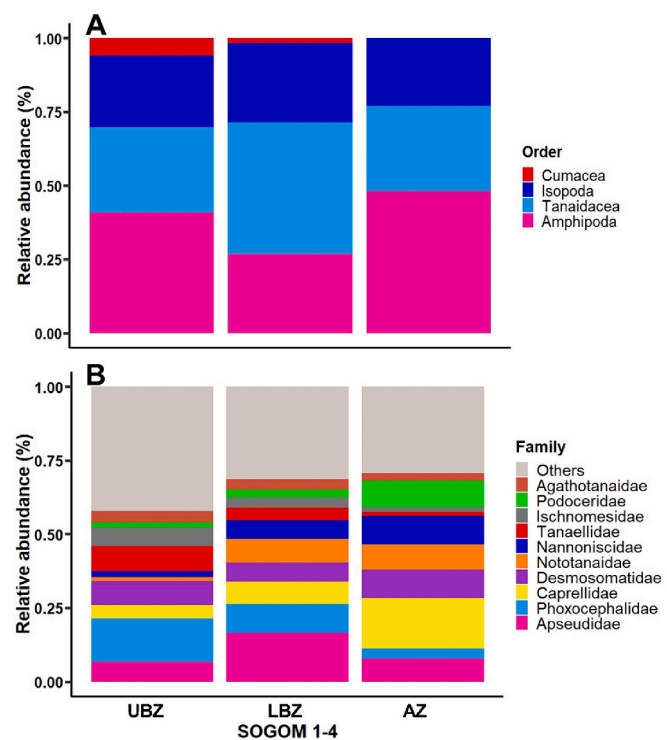
The numbers of sites grouped in the UBZ, LBZ, and AZ regions were 15, 29, and 19, respectively. The numbers of individuals collected from each region were 227, 326, and 131, respectively, whereas the numbers of families registered in each region were 40, 36, and 24, respectively (Table 1).

We collected and identified 684 specimens to the family level. They



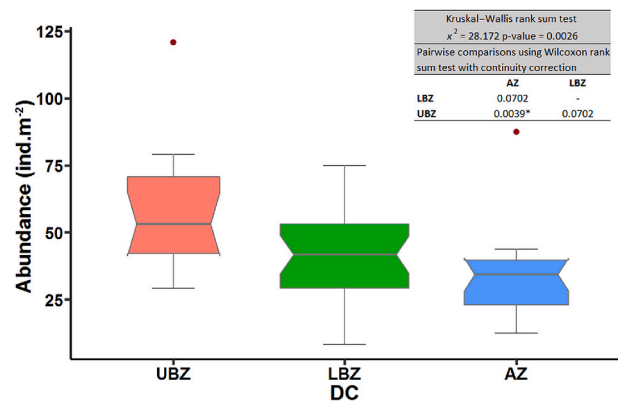


**Fig. 2.** Two-dimensional PCA ordinations of the environmental variables of SOGOM 1–4. PC1 and PC2 accounted for 70% of the variation. The graph shows the influence of the bathymetric gradient on environmental factors. UBZ registered the highest temperature and OM, PAH, and silt content, while AZ recorded the highest carbonate and DO content.



**Fig. 3. A-B.** Relative abundance of Peracarida members during SOGOM 1–4 based on depth. **A)** Orders. Amphipoda showed the highest relative abundance in UBZ and AZ, whereas Tanaidacea was the most abundant order in LBZ. **B)** Families. Phoxocephalidae, Apeudidae, and Caprellidae were the most abundant in UBZ, LBZ, and AZ, respectively. Abbreviations: Upper bathyal zone (UBZ); lower bathyal zone (LBZ); and abyssal zone (AZ).

belonged to 53 Peracarida families of four orders, namely, 19 from Amphipoda, 17 from Isopoda, 13 from Tanaidacea, and 4 from Cumacea. The most abundant orders of Peracarida were amphipods and tanaidaceans, representing 36.4% and 35.8% of total abundance, respectively, followed by isopods (25.1%). Cumaceans were the least abundant order (2.7%) (Fig. 3 A). The ten most abundant families in order were Apeudidae, Phoxocephalidae, Caprellidae, Desmosomatidae, Nototanaiidae, Nannoniscidae, Tanaellidae, Ischnomesidae, Podocерidae, and Agathotanaiidae, together accounting for 66% of the total relative abundance (Fig. 3 B). This general pattern presented variations



**Fig. 4.** Box plots of Peracarida abundance (ind. m<sup>-2</sup>) during SOGOM 1–4. Abundance of Peracarida decreased with increasing depth; however, a significant difference was observed only between UBZ and AZ.

depending on the depth. Tanaidacea was the most abundant order in the UBZ, whereas at the family level, Apeudidae was the most abundant one in the LBZ; Phoxocephalidae was the most abundant one in the UBZ, and Caprellidae was the most abundant one in the AZ. The families that registered the most records were Apeudidae, Phoxocephalidae, Desmosomatidae, Nannoniscidae, and Nototanaiidae, collected at 40, 38, 30, 27, and 27 sampling sites, respectively. In contrast, twenty families registered only a single record.

The standardized average abundance was 43 ind. m<sup>-2</sup>, ranging from 8 (site 35 in Campeche Canyon at 2621 m deep) to 121 ind. m<sup>-2</sup> (site 6 in the southern region at 1035 m deep).

We observed a decrease in the abundance with increasing depth (Figs. 4 and 5). A significant difference was observed only between the UBZ and AZ. In addition, four sites (56, 58, 23, and 59) registered higher abundance values than those of the adjacent sites in the bathymetric profile (Fig. 5).

Abbreviations: Depth category (DC); upper bathyal zone (UBZ); lower bathyal zone (LBZ); and abyssal zone (AZ). \* indicates significant difference

Site 6 exhibited the highest abundance. In general, high and intermediate abundance values were recorded in the northwestern region and Campeche salt domes zone. Intermediate and low values were observed in the remainder of the study area. Low abundance was recorded particularly in the abyssal zone. In addition, three of the southernmost and shallowest sites exhibited lower abundances (Fig. 6).

### 3.3. Multivariate analysis

The nMDS showed gradual compositional and structural community shifts throughout the analyzed bathymetric range (Fig. 7). The ANOSIM analysis supported these results because the global value, although relatively low (0.214), was significant ( $p = 0.001$ ). In addition, a comparison of the pairs allowed us to observe gradual bathymetric variations. All comparisons between the DC pairs were significant, and the highest difference was observed between the extremes of the analyzed range: UBZ-LBZ ( $R = 0.195$ ,  $p = 0.006$ ), LBZ-AZ ( $R = 0.167$ ,  $p = 0.002$ ), and UBZ-AZ ( $R = 0.328$ ,  $p = 0.001$ ). Although the nMDS showed a high stress value (0.26), the recorded values were considered acceptable because the site arrangement was consistent with the ANOSIM results. These results, clearly show the effect of the bathymetric gradient on the community structure.

Abbreviations: Depth category (DC); upper bathyal zone (UBZ, pink circles); lower bathyal zone (LBZ, green triangles); and abyssal zone (AZ, blue square). The sites are ordered according to the bathymetric gradient from lower left corner to upper right one

The major changes in the Peracarida community structure were attributed to the better representation of Phoxocephalidae and

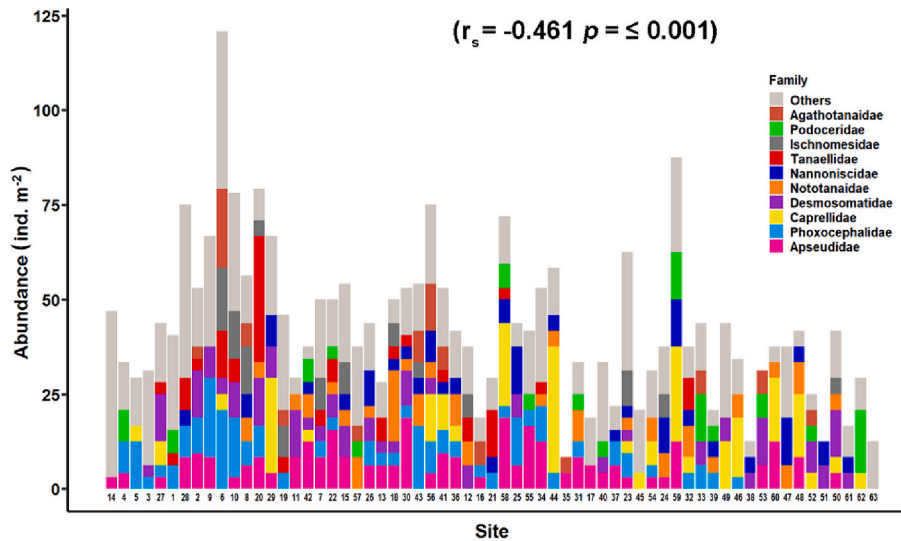


Fig. 5. Abundance of the Peracarida families based on depth during SOGOM 1–4.  $r_s$  = Spearman correlation. Sites are ordered from shallowest to deepest from left to right. Abundance showed a significant negative correlation with depth.

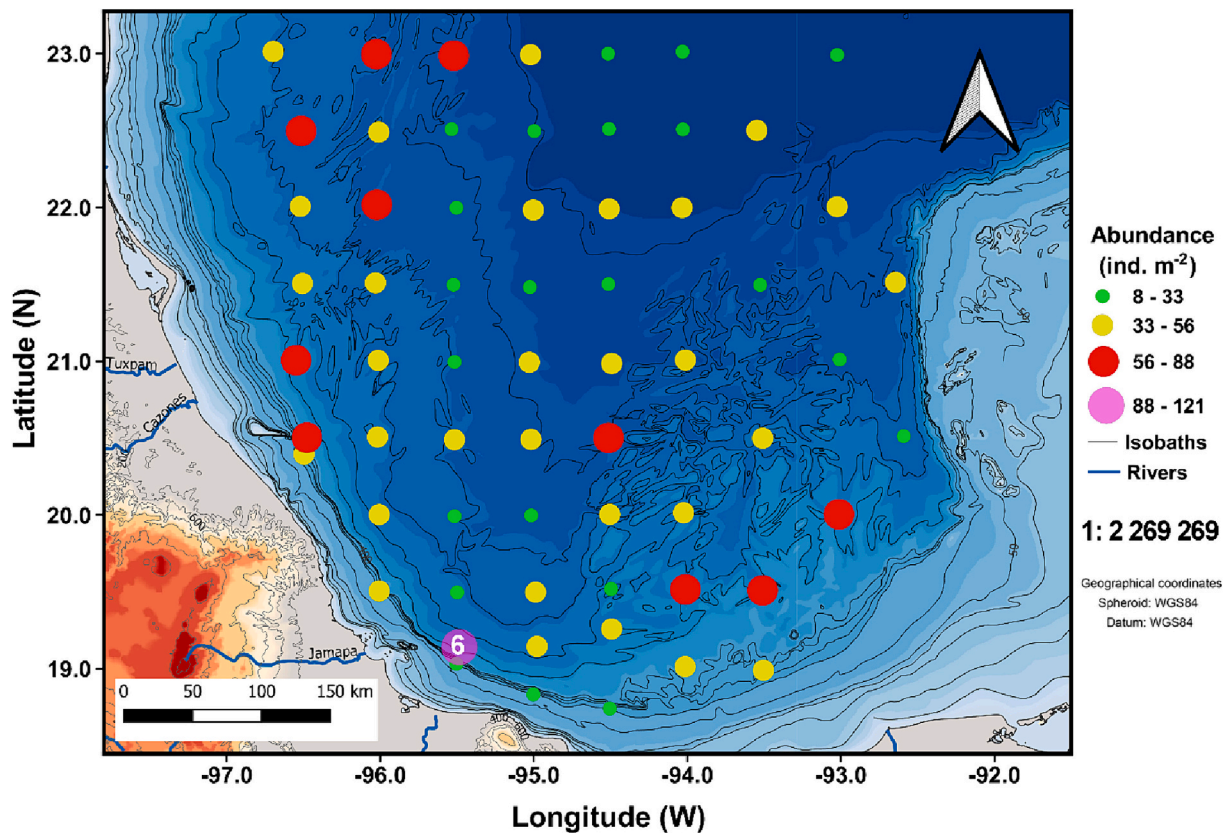


Fig. 6. Spatial distribution of Peracarida abundance during SOGOM 1–4. The southeast and northwest regions of the study area recorded the highest abundance values.

Ischnomesidae at sites in the upper bathyal region; Apeusidae and Agathotanaidae in the LBZ; and Desmosomatidae, Caprellidae, and Podoceridae in the AZ (Fig. 8).

Abbreviations: Upper bathyal zone (UBZ); lower bathyal zone (LBZ); and abyssal zone (AZ)

BIOENV analysis revealed the principal drivers of the Peracarida community. The four environmental parameters that showed the best match with the biotic similarity matrices using Spearman’s rank

correlation (0.32) were latitude, depth, temperature, and aliphatic hydrocarbons ( $p = 0.001$ ) without permuted statistics greater than Rho (Supplementary Data).

### 3.4. Diversity estimators

Diversity analysis (carried out at the family taxonomic level) showed that the UBZ was the most diverse depth category, followed by the LBZ,

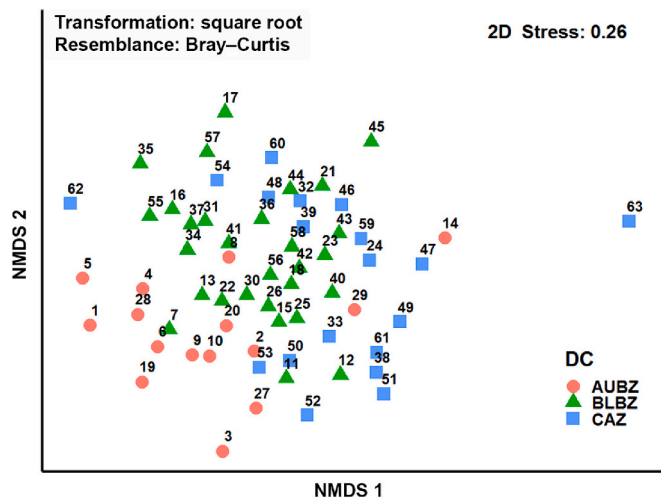


Fig. 7. Non-metric multidimensional scaling based on standardized abundance data and Bray-Curtis similarities.

while the least diverse was the AZ. The coverage-based R/E (rarefaction and extrapolation) sampling curves showed this pattern for the three estimators (Hill numbers,  $q = 0, 1, \text{ and } 2$ ) and a progressive decline in diversity with increasing depth (Fig. 9).

Abbreviations: Depth category (DC); upper bathyal zone (UBZ); lower bathyal zone (LBZ); and abyssal zone (AZ)

Sites 19, 23, and 40 exhibited high diversity values. In general, we observed low and intermediate diversity values across the entire study area, with the highest values observed in the southeastern and north-western regions (Fig. 10).

#### 4. Discussion

##### 4.1. Environmental analysis

The present study included the entire bathymetric range of the deep sea (200–3740 m) in the southwestern Gulf of Mexico. Both the environmental and faunal patterns explored in this study included the main seasonal and interannual variations occurring in the region. Environmental characterization revealed two zones (UBZ and LBZ-AZ) based on

the zonation of abiotic variables (salinity, dissolved oxygen, and temperature) associated with depth. The gradual change observed along the DCs was characterized by the highest values of temperature and organic matter, silt, and polycyclic aromatic hydrocarbon content in the UBZ; the highest values of oxygen and clay; and the lowest temperature and organic matter content in the AZ. These findings agreed with the environmental variable patterns documented in the study area (Rivas et al., 2005; Escobar-Briones and García-Villalobos, 2009; Díaz-Asencio et al., 2019; Quintanar-Retama et al., 2022) and were relevant to faunal pattern analysis. Variations in productivity, temperature, and diversity of sediment grain size with depth have been identified as fundamental in determining patterns of abundance, species richness, and turnover in the deep sea (Joydas et al., 2018; Rex, 1981). More detailed discussions of the environmental analysis results can be found in Armenteros et al. (2022) and Quintanar-Retama et al. (2023, 2022).

##### 4.2. Description of the fauna

Amphipoda was the most abundant order identified in our study. This finding is in line with those from studies carried in other seas (Brökeland et al., 2007; Di Franco et al., 2021) and in the GoM (Demopoulos et al., 2014; Hernández-Ávila et al., 2021); however, this is not a constant rule. Isopoda is usually reported as the dominant order (Brandt et al., 2005; Golovan et al., 2013) and amphipods have been recorded among the less abundant orders (Brandt et al., 2005). According to Golovan et al. (2013), the proportion of each Peracarida order in the deep sea varies considerably depending on the sampling depth and geographical location. In our study, we recorded a higher relative abundance of amphipods than of the other orders in the UBZ and AZ, whereas in the LBZ, Tanaidacea was the most abundant order. Isopods was not the most abundant order in any of the three depth categories in the southwestern GoM. Nonetheless, a bias introduced by the sampling gear in the assessment of the order composition cannot be overlooked. For example, when using an epibenthic sledge, which collects benthic organisms from the sediment-water interface (Flannery and Przeslawski, 2015), peracarids are usually the dominant taxon within the macrofauna (Brandt et al., 2005) and mysids and isopods are the most abundant orders (Almeida et al., 2017; Brandt et al., 2005). In our study, the use of a box corer made it difficult to capture groups such as isopods belonging to the Munnopsidae family, which have good swimming ability (Brandt et al., 2007a). The operation of this device generates a bow wave that

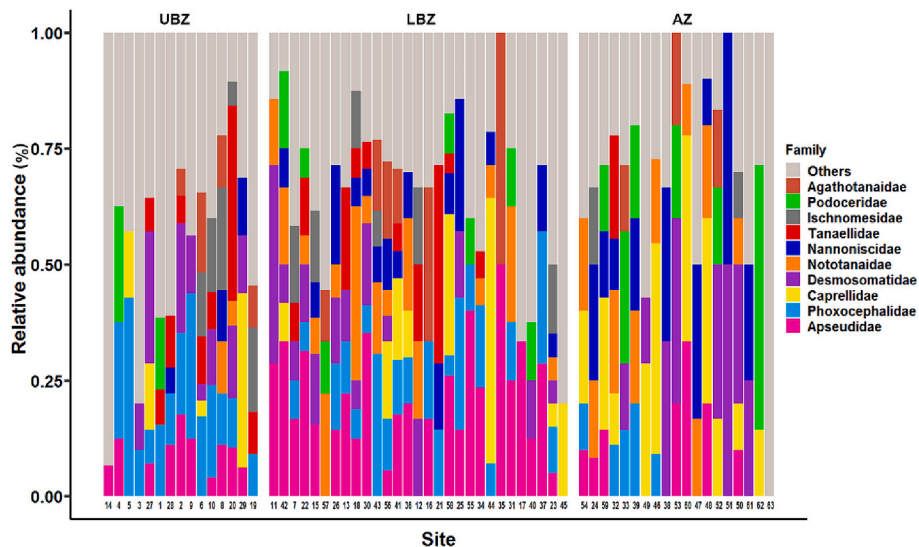


Fig. 8. Relative abundances of the Peracarida members along depth during SOGOM 1–4. Sites are ordered from shallowest to deepest from left to right. Phoxocephalids, apseudids, and caprellids dominated in most sites of UBZ, LBZ, and AZ, respectively. The high contribution of desmosomatids and nototanaids to the abundance in LBZ and AZ is shown.



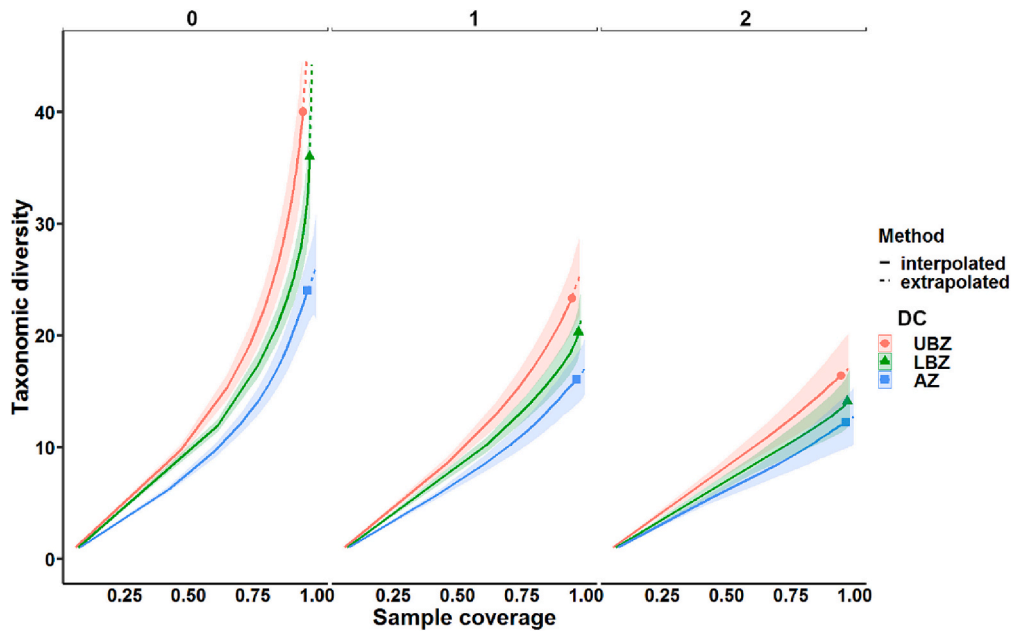


Fig. 9. Coverage-based R/E (rarefaction and extrapolation) sampling curves for the three Hill numbers ( $q = 0, 1,$  and  $2$ ). The three diversity orders decreased with increasing depth.

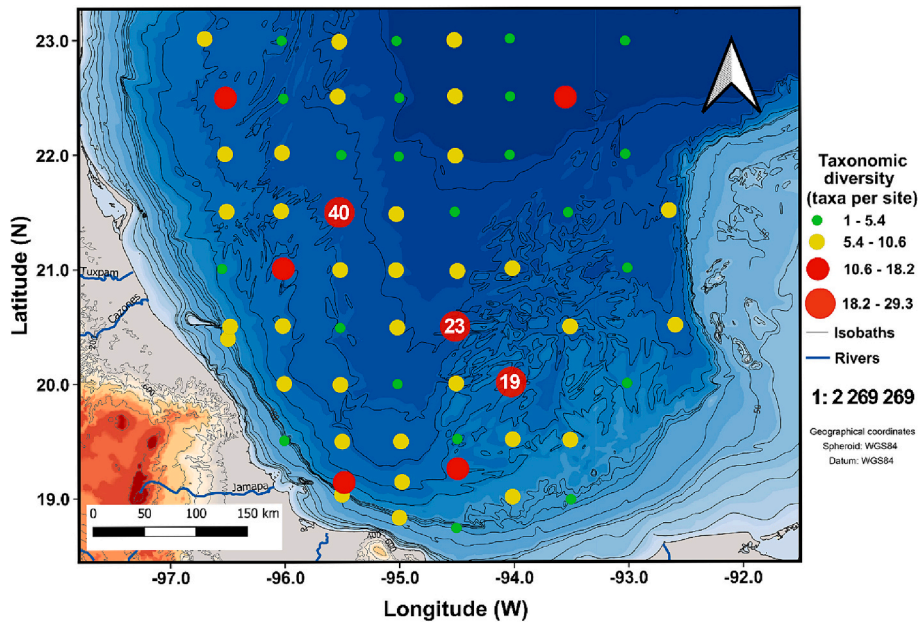


Fig. 10. Spatial distribution of Peracarida diversity values during SOGOM 1–4. The southeast and northwest regions of the study area recorded the highest diversity values.

likely disturbs the sediment surface (Montagna et al., 2017), displacing some epibenthic organisms from the sampled area, particularly those with good swimming abilities. Recent research in the north of the study area using the same type of device and same sized sediment sieving mesh as used by us (Hernández-Ávila et al., 2021) reported a ranking similar to that of our findings with respect to the contribution of the Peracarida orders to total abundance (Amphipoda, Tanaidacea, Isopoda, and Cumacea).

The ten most abundant families consisted of a diverse mix, with four families belonging to tanaidaceans (Apseudidae, Nototanaidae, Tanaellidae, and Agathotanaidae), three representing amphipods (Phoxocephalidae, Caprellidae, and Podoceridae), and the remaining

three falling under isopods (Desmosomatidae, Nannoniscidae, and Ischnomesidae). All of them were documented as well-represented taxa in the deep-sea (Blazewicz-Paszkwowycz et al., 2012; Frutos and Jazdzewska, 2019; Golovan et al., 2013). The most abundant family Apseudidae is the most plesiomorphic family as well, and has had time to disperse, adapt, and evolve in the bathyal region. The Leviapseudinae subfamily was only found in the deep-sea (at depths larger than 1000 m) (Blazewicz-Paszkwowycz et al., 2012) and we found at 186 m deep. Nototanaidae and Tanaellidae are well-represented families from the littoral to hadal zones, whereas Agathotanaidae shows predominantly abyssal and hadal distribution (Blazewicz-Paszkwowycz et al., 2012). In contrast, Phoxocephalidae and Desmosomatidae are widely distributed,

abundant, and specialized amphipod and isopod families, respectively, in the deep sea (Brandt et al., 2005, 2007b; Wilson, 2008; Golovan et al., 2013). Phoxocephalids are sediment-burrowing organisms that live in habitats extending from shallow coastal waters to abyssal zones (Shin, 2023). They are predators of other benthic invertebrates, especially those with soft bodies such as nematodes and polychaete annelids (Oliver et al., 1982). In contrast, desmosomatids have greater mobility capacity than those of phoxocephalids. Their anterior pereopods are ambulatory, and the three posterior pairs are slightly modified for swimming (George, 2001). They are considered moderate swimmers (Brix et al., 2020), and this taxon is globally distributed; its members occur in a wide bathymetric range, from shallow coastal waters to the abyssal zone (Golovan, 2018).

Among the 17 families of isopods, 10 belonged to the suborder Asellota, which has been documented as being highly dominant in the deep sea (Brandt et al., 2005, 2007a; Wilson, 2008). The five families with the highest number of records coincided with the most abundant families. Two were tanaidaceans (Apeudidae and Nototanaididae), one was an amphipod (Phoxocephalidae), and two were isopods (Desmosomatidae and Nannoniscidae). The family Paranarthreullidae (Błażewicz et al., 2019) constitutes a new record for the Gulf of Mexico registered at 2255 m depth. This is a typical deep-sea cosmopolitan taxon that has not yet been recorded on continental shelves. Its distribution ranges from the bathyal to hadal regions. The records nearest to the study area correspond to the North Atlantic.

We recorded lower abundance values than the observations made in the north of the GoM. Wei et al. (2012), registered an average abundance of 689 ind. m<sup>-2</sup> (ranging 27–16,567 ind. m<sup>-2</sup>) for amphipods, tanaidaceans, and isopods. We recorded an average abundance of 43 ind. m<sup>-2</sup> (ranging 8–121 ind. m<sup>-2</sup>). Wei et al. (2012) indicated the importance of organic carbon discharged by the Mississippi River in promoting high abundance. If the values of the six sites located in front of this river mouth are not considered, the average abundance drops to less than half, 315 ind. m<sup>-2</sup> (range: 27–1060 ind. m<sup>-2</sup>). Another factor for consideration is the smaller mesh size (300 µm, compared to 500 µm used by us) of the sieve. Thus, direct comparisons with other studies are not always possible, particularly when the devices used to collect samples are different. For example, epibenthic sledges are frequently used in deep-sea peracarid studies (e.g., Brandt et al., 2005; Golovan et al., 2013; Almeida et al., 2017). This device is ideal for biodiversity studies as it captures large numbers of specimens but makes quantitative analysis difficult because of the errors associated with calculating the hauling distance (Brenke, 2005; Brökeland et al., 2007; Golovan et al., 2013). Interestingly, Lins and Brandt (2020) pointed out that relative abundance data obtained using the epibenthic sledge and box corer can be comparable, and some diversity metrics such as evenness, estimated number of taxa, and Shannon diversity can be used if higher taxa are used. However, they also recommended caution when comparing data identified at the species level or from different areas.

The depth-related pattern of general abundance that we documented (abundance decreasing with increasing depth) agrees with that previously observed for macrofauna (Sanders, 1968; Gage and Tyler, 1991; Wei et al., 2010, 2012; Baldrighi et al., 2014; Bernardino et al., 2016) and peracarids in other seas (Golovan et al., 2013). This pattern has been recorded previously in the GoM (Wei et al., 2012) and was linked to OM availability with depth (Morse and Beazley, 2008) and distance from the coast (Escobar-Briones and García-Villalobos, 2009).

The spatial abundance pattern we found partially coincided with that reported for high-level macrofaunal taxa in this region (Quintanar-Retama et al., 2023). In both studies, the salt domes zone in Campeche Bay was identified as an area of high relative abundance, in addition to some sites in the central-western region of the study area. In our study, the intermediate and high values recorded in the eastern region could be explained, in part, by the OM contribution from the rivers on the Veracruz and Tamaulipas coasts (e.g., the Soto la Marina, Pánuco, Tuxpan, and Czones Rivers). Campeche Bay receives a significant OM

load from the Grijalva–Usumacinta system (Toledo-Ocampo, 2005). Furthermore, these sites are in areas with a high number of natural hydrocarbon seeps that support primary chemosynthetic producer communities (Sahling et al., 2016) and do not depend completely on the input of OM from surficial waters. Moreover, in this area, a cyclonic eddy occurs from July to April (Díaz-Flores et al., 2017; Pérez-Brunius et al., 2013), which promotes primary productivity and subsequent OM export to the GoM bottom. Together, these factors explain the high abundance observed in this zone. We recorded the lowest abundance values in the abyssal plain region, which was characterized by lower OM flow (Escobar-Briones and García-Villalobos, 2009) and the lowest OM content in the sediments, than those of other zones. Importantly, sampling was conducted during two climatic seasons: spring and summer. Although the gyre remains in Campeche Bay almost year-round, the magnitude of its influence varies throughout the year. Similarly, the contribution of the Grijalva–Usumacinta system varies between spring and summer. Thus, the average of the environmental value factors includes the possible seasonal and interannual variations of these variables in this region of the Gulf of Mexico.

#### 4.3. Multivariate analysis

ANOSIM and nMDS clearly showed shifts in the peracarid community structure and composition across the bathymetric gradient. Bathymetric variations in the composition and structure of the peracarid community have been documented in the study area (Hernández-Ávila et al., 2021) as well as in other regions (Brandt et al., 2016; Di Franco et al., 2021; Golovan et al., 2013). Latitude and depth were the environmental factors that showed a high correlation with the peracarid community distribution. Importantly, both factors have been registered as contributors to the structure of deep-sea peracarid communities (e.g., Di Franco et al., 2021). The third variable most closely related to the fauna was temperature. This is an important driver of benthic communities (Brown and Thatje, 2014) because of its influence on physiological processes (Clarke, 1998) that affect faunal zonation in the deep sea.

Among the depth-related variations in the composition of the Peracarida community, Phoxocephalidae and Caprellidae were well-represented in the UBZ and AZ, respectively. According to Frutos and Jazdzewska (2019), the conditions where caprellids settle are appropriate for filter feeders, whereas areas with lower proportion of fine sediments are more favorable for infaunal taxa such as phoxocephalids. In fact, in the UBZ, the sedimentation rate was higher than that in the AZ (Díaz-Ascencio et al., 2019), which could imply a less favorable environment for filter organisms, while in the AZ, it could be the opposite. In addition, we recorded an increase in clay and a decrease in silt content with increasing depth, which may favor the establishment of taxa such as Phoxocephalidae in the UBZ region. This might partially explain the distribution of these taxa in the study area.

#### 4.4. Diversity estimators

Diversity assessments at the species level require enormous resources in terms of time, money, and expertise. Faced with the accelerated loss of biodiversity (genes, species, and functional traits) and the consequent loss of ecosystem services (Cardinale et al., 2012), seeking alternatives is advised to evaluate diversity. These difficulties are accentuated in the fauna from areas with enormous gaps in sampling coverage, such as the deep sea (Clark et al., 2016). Furthermore, the difficulty of obtaining qualified taxonomists has increased (Giangrande, 2003). Several alternatives exist for this scenario, one of which is the use of molecular tools for species identification; however, the data available in GenBank are incipient (Alalykina and Polyakova, 2020). Another alternative is to use trophic guilds, which allow for studies on functional diversity. An additional option, taxonomic resolution reduction is perhaps the most common approach in ecological analyses (Ellis, 1985), and many studies have reported satisfactory results with it (Bett and Narayanaswamy,



2014; Checon and Amaral, 2017). To explore general patterns of diversity, assessment at the family taxonomic level has also been reported as an alternative. According to Zou et al. (2020), “recording family-level diversity can be a meaningful proxy for determining species-level diversity patterns in biodiversity studies.” They observed a high family–species diversity correlation in arthropod taxa. Meanwhile, Gomez Gesteira et al. (2003) concluded that family-level data are generally sufficient to monitor the effects of pollution in infralittoral soft-bottom environments. They obtained similar diversity values regardless of the use of species, genus, or family levels. Based on this, and given the need for basic information that could allow the assessment of the impact of human activities, such as the exploration and extraction of oil in a region where future hydrocarbon spill scenarios could occur, we are confident that for this initial effort, the diversity assessment identifying the fauna at the taxonomic family level is adequate.

The order Amphipoda had the largest number of families, as has been pointed out in other regions (Golovan et al., 2013). In the deep sea, the typical bathymetric diversity pattern consists of the highest diversity at intermediate depths (1500–2500 m) (Ramirez-Llodra et al., 2010; Sanders, 1968; Wei and Rowe, 2019). This pattern has also been recorded in polychaetes and higher taxa of macrofauna in the study area (Quintanar-Retama et al., 2023; Quintanar-Retama et al., 2022). However, in our study, we observed that the peracarid diversity showed a decreasing bathymetric pattern with increasing depth, which was consistent with the three calculated Hill numbers. These differences, with respect to the typical diversity pattern in the deep sea, have been previously documented and were related to the target taxon or regional changes (Shantharam and Baco, 2020).

Regions with higher diversity values identified in this study have been previously documented as high-diversity zones (Quintanar-Retama et al., 2023, Quintanar-Retama et al., 2022). Relatively low diversity values were observed at sites near the coastline and in the Campeche and Coatzacoalcos canyons, which could be related to the high sedimentation rates recorded at these sites (Díaz-Asencio et al., 2019). Low diversity and high dominance within peracarid communities have been previously documented in areas with important sedimentary dynamics (Almeida et al., 2017), which could explain the patterns observed in this region of the Gulf of Mexico.

## 5. Conclusions

The present study contributes to the global understanding of infaunal communities in the deep sea of the Gulf of Mexico and constitutes a baseline for further ecological studies on deep-sea peracarid fauna in this poorly studied region. We registered 4 orders and 53 Peracarida families. Amphipoda was the most abundant order (36.4% of the total peracarids total abundance) and registered the highest number of families (19). The abundance pattern was related to depth (decreased with increasing depth) and also to the regional conditions of the study area, showing two zones with greater abundance of peracarids (the salt domes zone in Campeche Bay and the western region). The two zones share some characteristics, such as the influence of rivers that provide sediments and the presence of hydrocarbon natural seeps. The composition and structure of the peracarid community showed shifts along the analyzed bathymetric range. The abiotic factors most related to fauna distribution were latitude, depth, temperature, and sediment aliphatic hydrocarbon content. The bathymetric diversity analysis showed results consistent with those of the three calculated diversity orders. The UBZ was the most diverse, followed by the LBZ; the AZ was the least diverse. Higher diversity values were recorded at sites located in the southern and western regions of the study area and in the salt domes zone of Campeche Bay.

## CRedit authorship contribution statement

**Octavio Quintanar-Retama:** Writing – review & editing, Writing –

original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ana Rosa Vázquez-Bader:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Adolfo Gracia:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2024.103977>.

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