Continental Shelf Research 198 (2020) 104098

Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: http://www.elsevier.com/locate/csr

Research papers

# Influence of bottom environment conditions and hydrographic variability on spatiotemporal trends of macrofaunal amphipods on the Yucatan continental shelf

Carlos E. Paz-Ríos [a,*], Daniel Pech [a], Ismael Mariño-Tapia [b,1], Nuno Simões [c,d,e]

[a] Laboratorio de Biodiversidad Marina y Cambio Climático (BIOMARCCA), El Colegio de La Frontera Sur, Unidad Campeche, 24500, Lerma, Campeche, Mexico
[b] Centro de Investigación y de Estudios Avanzados Del Instituto Politécnico Nacional, Unidad Mérida, Cordemex, 97310, Mérida, Yucatán, Mexico
[c] Universidad Nacional Autónoma de México, Facultad de Ciencias, Unidad Academica Sisal, 97356, Sisal, Yucatán, Mexico
[d] Laboratorio Nacional de Resiliencia Costera, Puerto de Abrigo, Sisal, Yucatán, Mexico
[e] International Chair for Ocean and Coastal Studies, Harte Research Institute, Texas A & M, Corpus Christi, TX, USA

A R T I C L E  I N F O

*Keywords:*
Soft-sediment
Community ecology
Amphipoda
Gulf of Mexico
Upwelling
Distribution pattern

A B S T R A C T

Amphipod species collected during three oceanographic campaigns (2010–2012) were analyzed to describe their spatiotemporal community distribution trends and their relationships with bottom water and sediment variables. The results show that the species richness (117 spp.) did not reach its maximum value according to the species accumulation curve (up to 187 spp.). Multivariate analyses and constrained ordinations techniques detected three main amphipod assemblages along the longitudinal gradient (i.e., Western Caribbean, Mid-Yucatan, and West-Yucatan) and during two temporal hydrographic scenarios (i.e., upwelling in 2010–2011 and non-upwelling in 2012). In 2010–2011, low values in species richness and abundance from the Western Caribbean and eastern Mid-Yucatan assemblages were associated with relatively low bottom-water temperatures from the upwelling systems. In 2012, the absence of upwelling and the occurrence of a warm-core anticyclonic eddy seemed to cause an increase in species richness and abundance in the three assemblages. The hydrographic variability and sediment characteristics are suggested as the major environmental drivers that shapes the soft-bottom amphipod community structure and diversity in the Yucatan continental shelf.

## 1. Introduction

The description and comprehension of benthic macrofauna distribution includes the understanding of the relative importance of diverse factors (e.g., sediment texture, food availability) and processes (e.g., recruitment, dispersal) that shape the spatial and temporal distribution trends on the species composition and abundance (Constable, 1999; Kraufvelin et al., 2011). Marked changes in such factors and processes are commonly assumed to result in significant changes in community characteristics (Dauvin et al., 2004; Hewitt et al., 2005; Pitcher et al., 2012). However, the importance of ecological drivers in explaining causality on benthic macrofauna distribution relies on its pervasive control on large spatial extensions and the complete range of biological hierarchies in the community structure (Zajac et al., 1998; Hernández-Arana et al., 2003; Pitcher et al., 2012), as well as in the function of environmental and geographical gradients.

In this study, we analyze the spatiotemporal variability of the amphipod community on the Yucatan continental shelf (YCS) using environmental factors such as sediment characteristics and bottom-water hydrography as a function of depth and longitudinal gradients. Amphipods are benthic crustaceans with a high morphological diversity, different lifestyles, feeding modes, functional key roles on the water-sediment interface habitats (Sanz-Lázaro and Marín, 2011; Arfianti and Costello, 2019), and constitute the second most dominant taxon in the macrofauna, after polychaetes, on the soft-sediment habitats from the YCS (Hernandez-Avila et al., 2020). Also, amphipods represent potential preys capable to modulate the abundance and distribution of benthic, demersal, and pelagic predators (Highsmith and Coyle, 1991; Link et al., 2002; Soliman and Rowe, 2008; Demchenko et al., 2016).

The benthic amphipods complete their entire life-cycle in the

* Corresponding author. Laboratorio de Biodiversidad Marina y Cambio Climático (BIOMARCCA), El Colegio de la Frontera Sur, Av. Rancho Polígono 2-A, Col. Ciudad Industrial, C.P. 24500, Lerma, Campeche, Mexico.
*E-mail address:* cepaz@ecosur.edu.mx (C.E. Paz-Ríos).
[1] Present address: Universidad Nacional Autónoma de México, Escuela Nacional de Estudios Superiores, Unidad Mérida, 97357 Ucú, Yucatán, México.

https://doi.org/10.1016/j.csr.2020.104098
Received 22 July 2019; Received in revised form 4 March 2020; Accepted 9 March 2020
Available online 10 March 2020
0278-4343/

sediment displaying a direct development mode (i.e., lack extended planktonic larval stages), local recruitment, and parental care (Johnson et al., 2001). Hence, their life-cycle traits have been suggested as closely linked to changes in bottom environmental characteristics (Sainte-Marie, 1991; Conlan, 1994). Benthic amphipods are a taxonomic group with diverse ecological requirements and considered as a proxy to explore hypotheses on the environmental drivers shaping marine biodiversity trends. The direct influence of the bottom environmental conditions, over the amphipod community characteristics, has been used to assess the ecological status of soft-sediment benthic habitats impacted by human-induced disturbances (Gómez-Gesteira and Dauvin, 2000; Marsden and Rainbow, 2004; Dauvin and Ruellet, 2007).

The karstic nature and sediment characteristics on the YCS provide a mosaic of potential spaces to maintain diverse benthic macrofauna assemblages, and hence to impact largely the distribution patterns of abundance and species composition (Hernández-Arana et al., 2003; Domínguez-Castanedo et al., 2007; Santibañez-Aguascalientes et al., 2018), as has been noticed on other similar shelves (Williams et al., 2010; Zajac et al., 2013; Henkel and Politano, 2017). Previous studies on benthic macrofauna of shallow habitats in the YCS have highlighted changes in community attributes and species composition as an adaptive response to the environmental variability of nearshore ecosystems, e.g., beach, lagoon (Pech et al., 2007; Hernández-Guevara et al., 2008; Rodríguez-Pliego et al., 2011; Paz-Ríos and Ardisson, 2018) and spatial complexity (Paz-Ríos et al., 2019). First insights on the spatial distribution of macrofauna in soft-sediment habitats of the YCS show a decreasing trends in species richness, abundance, and biomass when depth increases on soft-sediment habitats (Escobar-Briones and Falcon, 2005; Wei et al., 2012), especially in subtidal habitats near coral reef systems (Escobar-Briones and Jiménez-Guadarrama, 2010).

The YCS is a smooth, broad platform with carbonate sediments of variable texture and complex seabed topography (Logan et al., 1969; Balsam and Beeson, 2003), with high hydrographic variability due to dominant westward circulation, water masses with different thermohaline properties, and upwelling systems (Enriquez et al., 2013; Ruiz-Castillo et al., 2016). These hydrographic characteristics could shape the diversity and abundance of amphipods (Paz-Ríos, 2008; Paz-Ríos and Pech, 2019), and the all benthic community (Hernandez-Avila et al., 2020). Here, as a first approach to understanding the spatiotemporal variability of benthic invertebrates in the YCS, we analyzed the distribution of amphipod community, one of the most frequent and abundant taxon on the YCS, and their attributes and species composition in view of the area's bottom water hydrography and sediment characteristics.

## 2. Materials and methods

### 2.1. Study area

The YCS, Gulf of Mexico, between −86.5° and −92.5° W and 20.7° and 24° N (Fig. 1), is a submerged northeastward extension (~300 km) of the Yucatan Peninsula gentle slope karst block (~1:1600) (Logan et al., 1969). The block was formed by recent Holocene sediments of lithified limestone with a high content of calcium carbonate (>75%) and is divided into two major submarine terraces: the inner (<60 m) and outer shelf (60–210 m) (Williams, 1963; Logan et al., 1969; Balsam and Beeson, 2003). The deposition of coralline skeletons and other calcareous minerals on the continental shelf has led to the formation of carbonate submerged cays and banks, islands, and coral reefs (Tunnell et al., 2007).

Three thermohaline water masses occur on the YCS: i) the Yucatan Sea Water mass (~26–31 °C, ~36.4–36.8 PSU) dominating the northern inshore of the YCS, ii) the Caribbean Subtropical Underwater mass (~22–26 °C, ~36.4–36.7 PSU) upwelled at the eastern edge and dominating the northern and eastern offshore region, and iii) the Gulf Common Water mass (~22.5 °C, ~36.3–36.5 PSU) prevailing at the whole offshore region of the YCS (Enriquez et al., 2013). The circulation

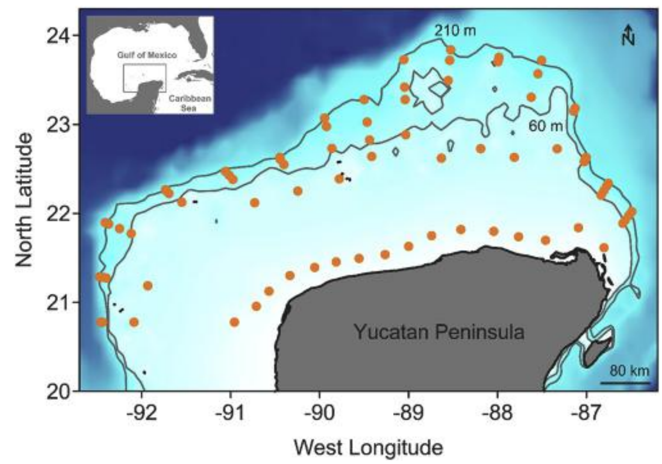


**Fig. 1.** Location of the sampling sites in the Yucatan continental shelf, southern Gulf of Mexico. Isobaths represent the upper limit of depth strata defined in Logan et al. (1969) for the inner shelf (60 m) and outer shelf (210 m). Coastline and bathymetry data were sourced from NOAA (https://www.ngdc.noaa.gov/mgg/bathymetry/relief.html).

in the YCS has a dominant westward direction with average speeds of 0.2–0.4 m $s^{-1}$ and is influenced by the easterly winds and by the Yucatan Current to a lesser extent (Enriquez et al., 2010; Ruiz-Castillo et al., 2016). The strong Yucatan Current, which flows through the Yucatan Channel with speeds of up to 2 m $s^{-1}$, generates an intense upwelling at the eastern shelf (Cabo Catoche) that modifies several properties of the seawater, including the temperature, oxygen, and nutrients (Reyes-Mendoza et al., 2016; Carrillo et al., 2017). The upwelling has a strong seasonal signal, being active only during spring and summer, i.e., March–September (Merino, 1997). The environmental variability in the YCS includes a period of frontal winter storms from approximately October to February (Zavala-Hidalgo et al., 2002) that are characterized by cold, intense winds from the north and/or northeast, with speeds of up to 25 m $s^{-1}$ (Enriquez et al., 2010). This affects the physical characteristics of the inner shelf water masses, with a marked decrease in temperature and generating high wave energy and strong mixing. Due to these effects, the winter frontal storms induce a disruption of the water column stratification and upwelling events (Reyes-Mendoza et al., 2016; Ruiz-Castillo et al., 2016).

### 2.2. Sampling procedure

Sediment samples were collected using a Smith-McIntyre grab (0.1 $m^2$) in three oceanographic campaigns (GOMEX) annually accomplished (11–21 September 2010, 23 September–3 October 2011, 27 November–8 December 2012) onboard the R/V Justo Sierra. Eighty stations were sampled during each campaign distributed through 16 transects (five per transect) perpendicular to the shore (Fig. 1). Organisms were obtained from three sediment subsamples using PVC cores of 5 cm in diameter and 10 cm in depth. On board, subsamples were anesthetized with magnesium chloride and seawater for 10 min and then were fixed with 10% formalin. In the laboratory, subsamples were washed with freshwater and sieved through a 500 μm screen. The retained macrofauna was preserved in 70% ethanol and then sorted by higher taxonomic categories (i.e., polychaetes, amphipods, tanaidaceans, ostracods, sipunculids, isopods, bivalves, gastropods, decapods, and other miscellaneous taxa). For the purpose of this work only the amphipods were counted and identified to the lowest taxonomic category. An additional sediment subsample was taken for sediment characteristic analysis, measured as texture using the relative contribution of grain size classes (i.e., sand, silt, and clay), following Bouyoucos's (1962) method, and organic carbon content following the Gaudette et al. (1974) method. The temperature (°C), salinity (PSU), dissolved oxygen (ml $l^{-1}$), and chlorophyll-*a* (mg $m^{-3}$) of the bottom water (~5–10 m above seabed) were recorded in-situ using a CTD Seabird 9 plus®.

### 2.3. Data analysis

Sample-based species accumulation curves were calculated using presence/absence data from the three sampling periods. The species accumulation curves were calculated using the Chao 2 index in the software EstimateS 9 (Colwell, 2013) to obtain the estimated species richness as a function of the sampling year, and compared using a *t*-statistic.

To test whether community attributes (i.e., species richness and abundance) and species composition changed as a function of year and/or geographical longitude, a two-way factorial design was performed using the year and geographical longitude as fixed orthogonal factors, and the depth as a covariate. Three years were evaluated (i.e., 2010, 2011, and 2012) and the geographical longitude was evaluated in seven instances represented by one degree of West longitude amplitude (i.e., −86, −87, −88, −89, −90, −91, and −92). The covariate depth was represented by a bathymetric gradient from inshore to offshore and using the depth at which the samples were taken. This design was applied separately to analyze the community attributes using a permutational multivariate analysis of variance (PERMANOVA) test at a univariate mode and to analyze the species composition by using the standard mode of PERMANOVA. The univariate mode was done using a Euclidean distance matrix generated for both the species richness and total abundance per site. The standard mode was done using a zero-adjusted Bray-Curtis resemblance matrix (Clarke and Gorley, 2016) generated from a matrix of species composition and relative abundance that was transformed into the fourth root. Both modes of analyses were computed with 9999 permutations of residuals in a reduced model. Pairwise tests using a *t*-statistic were used to identify the differences between factor levels.

The spatiotemporal trend of the species composition and relative abundance was visually explored using a canonical analysis of principal coordinates (CAP) on the Bray-Curtis resemblance matrix. The CAP is a constrained ordination technique that considers the correlation structure among species (Anderson and Willis, 2003), using here the year and geographical longitude as predictive factors. An additional CAP was performed to display the ordination of sampling sites for the environmental characteristics by using normalized variables of bottom water and sediment (previous transformation of sediment data into arcsine) and a resemblance matrix for Euclidean distance. Variables showing autocorrelation were excluded.

A similarity percentage (SIMPER) analysis was carried out to determine the sets of species that characterize the different groups of samples (i.e., year and geographic longitude), using a cumulative contribution of 75% (Clarke, 1993). PERMANOVA, CAP, and SIMPER were performed in the PRIMER V7 & PERMANOVA add on (Anderson et al., 2008; Clarke and Gorley, 2016).

The potential relationship between the species matrix of abundances and environmental variables was explored using canonical correspondence analysis (CCA), with the forward selection and Monte Carlo method with 9999 permutations applied for determining predictive factors. The CCA was performed in Canoco V4.5 & CanoDraw V4 (ter Braak and Šmilauer, 2002).

## 3. Results

### 3.1. Species diversity

A total of 1120 organisms belonging to 117 species were obtained during the three sampling years. The most frequent and abundant amphipods were *Americhelidium americanum*, *Ampelisca agassizi*, *Ampelisca vadorum*, *Batea cuspidata*, *Erichtonius punctatus*, *Gibberosus myersi*, *Lembos unifasciatus*, *Gammaropsis elvirae*, *Meximaera diffidentia*, and *Rudilemboides naglei*.

The species accumulation curves, using the three years of data, show an estimate in species richness between 146 and 187 spp., higher than observed species richness (Fig. 2a). When considering each year separately, the estimated species accumulation curves increased annually ($p < 0.01$, in all cases) and also the cumulative number of species observed, thereby showing that 2010 had the lowest estimated value, and 2012 period had the highest accumulation (Fig. 2b). The curves never reached the asymptote, thereby suggesting the amphipod species diversity has the potential to be higher in the YCS.

### 3.2. Spatiotemporal variability of community characteristics

Species richness and abundance changed as a function of the geographic longitude, and only the abundance changed as a function of the sample year (Table 1) according to the univariate mode of PERMANOVA. The analysis also showed a higher abundance and species richness in shallow sites of the inner shelf (Fig. 3). The pairwise tests between sample years showed significant changes in abundance from 2010 (25 ± 8 ind. 60 $cm^2$) to 2012 (86 ± 27 ind. 60 $cm^2$) (Fig. 4a). The pairwise tests between geographic longitudes showed that the highest values of abundance and species richness were maintained between the −90 (107 ± 41 ind. 60 $cm^2$) and −89 (28 ± 5 spp. 60 $cm^2$) longitudes, in the central sector of the YCS (Fig. 4b and c).

The species composition changed as a function of both the sample year and geographic longitude (Table 2) according to the standard mode of PERMANOVA. The analysis also shows that the amphipod community structure is influenced by the interaction of depth with geographical longitude. The pairwise tests between sample years showed that the species composition in 2012 significantly differed from the compositions observed in 2010 ($p = 0.018$) and 2011 ($p = 0.032$); but no between the 2010 and 2011 composition. The pairwise tests between geographic longitudes (Table 3) suggested the existence of three different amphipod assemblages grouped by longitudes; there were no significant differences in species composition between the −86 and −87 longitudes, between the −88, −89, and −90 longitudes, and between the −91 and −92 longitudes.

Despite the temporal variability in the species composition (Fig. 5a), the CAP ordination showed the formation of the three homogeneous amphipod assemblage as a function of the geographic longitude (Fig. 5b), similarly to the groups observed in the pairwise test. The first assemblage was located in the eastern sites of the YCS (i.e., −86, −87) named Western Caribbean; the second one was located at the central sites (i.e., −88, −89, −90) named Mid-Yucatan; and the third one was located at the western sites (i.e., −91, −92) named West-Yucatan. According to the SIMPER analysis, the species that contributed most to the entire community structure for 2010–2011 were: *Ampelisca agassizi*, *Ampelisca vadorum*, *Batea cuspidata*, *Bemlos* sp., *Erichtonius punctatus*, *Gammaropsis elvirae, Harpinia* sp., *Lysianopsis alba*, *Meximaera diffidentia*, *Neomegamphopus kalanii*, *Phtisica marina*, *Rudilemboides naglei*, and *Unciola serrata*. For 2012, the species were: *Americhelidium americanum*, *Ampelisca agassizi*, *Ampelisca vadorum*, *Bemlos spinicarpus*, *Gibberosus myersi*, *Harpinia* sp., *Lembos unifasciatus*, and *Rudilemboides naglei*. The average dissimilarity between all pairs of sites from 2010–2011 to 2012 was 98%. In the spatial dimension, the SIMPER analysis reveals that the Western Caribbean assemblage was characterized by *Americhelidium americanum*, *Ampelisca agassizi*, *Ceradocus shoemakeri*, *Metharpinia floridana*, *Meximaera diffidentia*, *Pedicorophium laminosum*, and *Rudilemboides naglei*; the Mid-Yucatan assemblage by *Americhelidium americanum*, *Ampelisca vadorum*, *Batea cuspidate*, *Erichtonius punctatus*, *Gammaropsis elvirae*, *Gibberosus myersi*, *Harpinia* sp., *Lembos unifasciatus*, *Metaprotella hummelincki*, *Phtisica marina*, and *Rudilemboides naglei*; and the West-Yucatan assemblage by *Ampelisca agassizi*, *Harpinia* sp., *Lysianopsis alba*, and *Unciola serrata*. The average dissimilarity between all pairs of sites was 98% between the Western Caribbean and Mid-Yucatan, and 99% between the Mid-Yucatan and West-Yucatan.

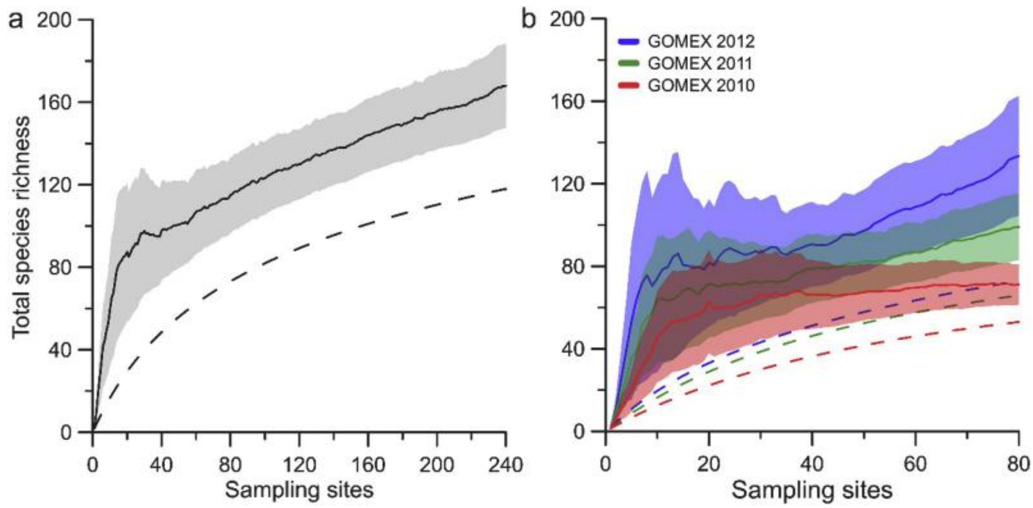


**Fig. 2.** Sample-based species accumulation curves from the three study years pooled together (a) and by year (b), based on the observed and estimated species richness. The solid line represents the estimated average values of the Chao 2 index; the shaded area represents ±1 SD of the Chao 2 index based on 100 randomizations; the dashed line represents the cumulative number of the observed species richness.

**Table 1**
Permutational multivariate analysis of variance (PERMANOVA) on the community attributes of amphipods based on an orthogonal two-factor model, with depth as a covariate. D: depth; Y: year; L: geographic longitude.

| Source | df | MS | *F* | p(perm) |
|---|---|---|---|---|
| Species richness | | | | |
| D (covariate) | 1 | 285.35 | 38.426 | **0.0001** |
| Y | 2 | 19.05 | 2.565 | 0.0769 |
| L | 6 | 29.26 | 3.941 | **0.0010** |
| D x Y | 2 | 9.69 | 1.305 | 0.2720 |
| D x L | 6 | 21.14 | 2.847 | **0.0148** |
| Y x L | 12 | 8.78 | 1.182 | 0.2902 |
| D x Y x L | 12 | 5.09 | 0.686 | 0.7321 |
| Residual | 198 | 7.42 | | |
| Total | 239 | | | |
| Abundance | | | | |
| D (covariate) | 1 | 2176.40 | 12.492 | **0.0048** |
| Y | 2 | 572.22 | 3.284 | **0.0278** |
| L | 6 | 385.44 | 2.212 | **0.0388** |
| D x Y | 2 | 343.45 | 1.971 | 0.1425 |
| D x L | 6 | 217.35 | 1.247 | 0.2628 |
| Y x L | 12 | 235.77 | 1.353 | 0.1955 |
| D x Y x L | 12 | 114.11 | 0.654 | 0.5805 |
| Residual | 198 | 174.23 | | |
| Total | 239 | | | |

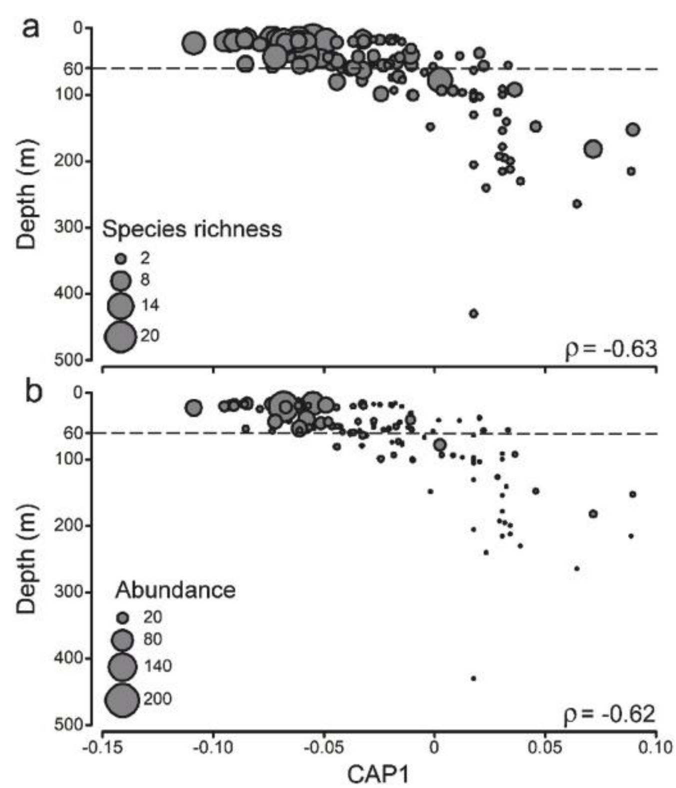


**Fig. 3.** Ordination of the sampling sites along the depth gradient with fitted values of the species richness (a) and abundance (b) per site. The dashed line represents the upper limit for the inner shelf. Spearman rank correlations (ρ) represent partial correlations (depth fixed as a covariate) between community attributes and the ordination axis 1 of the canonical analysis of principal coordinates (CAP).

### *3.3. Bottom environmental conditions*

The bottom water characteristics were similar in 2010 and 2011 (higher concentrations of chlorophyll-*a* and dissolved oxygen), but not in 2012 according to the CAP ordination (Fig. 6a). The ordination as a function of the geographic longitude (Fig. 6b) reveals that the bottom water characteristics (temperature and concentrations of chlorophyll-*a*) and sediment texture were roughly grouped into three similar associations like those observed in the species assemblages: Western Caribbean, Mid-Yucatan, and West-Yucatan. The sediment texture was a main factor contributing to the observed change along geographic longitude, showing a large sand content in the Western Caribbean and Mid-Yucatan, increasing the clay content towards the West-Yucatan. The Western Caribbean was characterized by lower values of temperature, whereas the Mid-Yucatan and Western Caribbean too by higher eastward values of chlorophyll-*a*. Differences on the measured environmental variables were observed among longitudinal geographic groups (Table 4).

A close analysis of the bottom-water temperature, using the 22.5 °C isotherm as a tracer for upwelled water in the YCS according to Merino (1997), showed a spatiotemporal variability that was clearly associated with the upwelling systems towards the eastern border in 2010, while in 2011 the upwelling effect was more extensive on the eastern inner shelf (Fig. 7). In 2012, no evidence of upwelling systems was observed. In 2010–2011, the upwelling was associated with a westward circulation

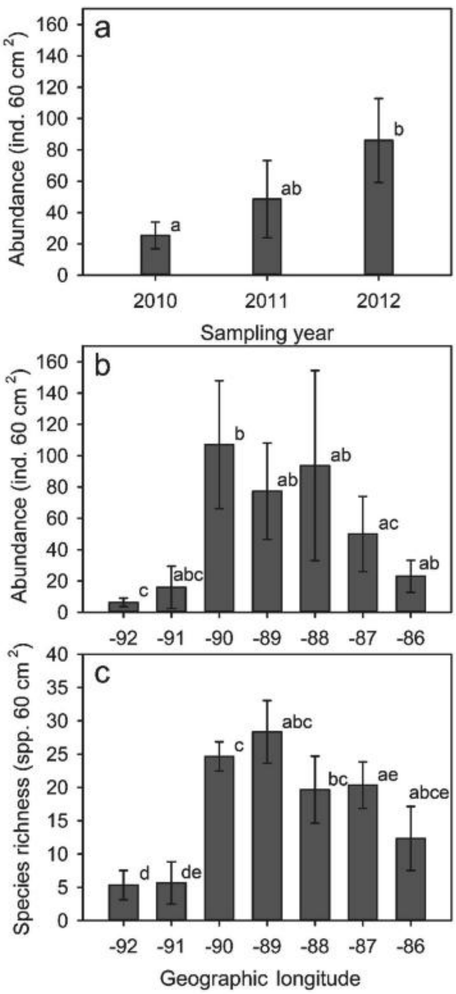


**Fig. 4.** Average value (±S.E.) of community attributes with observed significant changes from one-way permutational multivariate analysis of variance (PERMANOVA) per sampling year and geographic longitude. Distinct letters for the factor levels indicate significant differences at a critical value of α = 0.05.

**Table 2**
Permutational multivariate analysis of variance (PERMANOVA) on the composition and abundances of the amphipod community based on an orthogonal two-factor model, with depth as a covariate. D: depth; Y: year; L: geographic longitude.

| Source | df | MS | *F* | p(perm) |
|---|---|---|---|---|
| D (covariate) | 1 | 19767 | 14.041 | **0.0001** |
| Y | 2 | 3594 | 2.552 | **0.0009** |
| L | 6 | 3417 | 2.426 | **0.0001** |
| D x Y | 2 | 1849 | 1.313 | 0.1357 |
| D x L | 6 | 2143 | 1.522 | **0.0126** |
| Y x L | 12 | 1493 | 1.060 | 0.2770 |
| D x Y x L | 12 | 985 | 0.699 | 0.9902 |
| Residual | 198 | 1408 | | |
| Total | 239 | | | |

that generated a bottom-water longitudinal temperature gradient. Different temperatures were observed on the inner/outer shelf in the Western Caribbean (21–26/15–22 °C), Mid-Yucatan (21–29/16–25 °C), and West-Yucatan (24–27/16–26 °C) (Fig. 7a and b). A vertical profile of the water column in the Western Caribbean showed the 22.5 °C isotherm at a depth of ~60 m and 170 km from the shore in 2010 (Fig. 7d) and at an ~45 m depth and 120 km from the shore in 2011. During 2012, the bottom-water temperature shows a lower variability with a weak

**Table 3**
Pairwise tests between geographic longitudes from the standard mode of the permutational multivariate analysis of variance (PERMANOVA).

| Longitude | *t* | p(perm) |
|---|---|---|
| −86, −87 | 1.2140 | 0.1049 |
| −87, −88 | 2.0222 | **0.0001** |
| −88, −89 | 1.2875 | 0.0689 |
| −89, −90 | 1.0064 | 0.3862 |
| −90, −91 | 1.8649 | **0.0034** |
| −91, −92 | 1.2652 | 0.1096 |

stratification on the outer shelf, at a >100 m depth and at 190 km from the shore (Fig. 7c, f) and with temperatures between 24–26 °C on the inner shelf and 14–26 °C on the outer shelf. The rise of bottom-water temperatures (26 °C) in the Western Caribbean was associated with a warm-core anticyclonic eddy that developed approximately in 23° N and −88° W (Fig. 7c). This eddy was persistent through the entire sampling campaign and was characterized by warmer water and a lower salinity (35.8 PSU) than the adjacent sea (36.5 PSU).

### *3.4. Species assemblages and environmental characteristics*

A first CCA analysis was performed using data from 2010 and 2011 due to the similar amphipod community structure. A second CCA analysis was performed using only the 2012 data. Both analyses were based on the three identified species assemblages in the CAP analysis (i.e., Western Caribbean, Mid-Yucatan, and West-Yucatan) and two bathymetric strata: inner shelf (<60 m) and outer shelf (60–210 m). In both analyses, the results showed that the species composition and abundance were markedly structured as a function of depth, with a lower variability on the outer shelf (Fig. 8). The selected environmental variables explained more of the 70% of the variance (i.e., 84% in 2010–2011 and 73% in 2012).

According to the CCA of 2010–2011 (Fig. 8a), low abundances were related to high chlorophyll-*a* concentrations ($p = 0.0028$) in the Western Caribbean and some sites in the Mid-Yucatan inner shelf. The highest amphipod abundance was observed at the Mid-Yucatan inner shelf and was associated with relatively high bottom-water temperatures ($p = 0.0001$). The CCA of 2012 (Fig. 8b) showed that the abundance on the Western Caribbean inner shelf presented high values associated with high bottom-water temperatures ($p = 0.0001$) and low clay content in sediment ($p = 0.0086$). The highest amphipod abundance was observed at the Mid-Yucatan inner shelf and was associated with high values of organic matter content in sediment ($p = 0.0001$), high concentrations of dissolved oxygen ($p = 0.0026$), and low clay content in sediment. At the inner shelf of the West-Yucatan, higher amphipod abundances were associated with low contents of clay and organic matter in sediment ($p = 0.0001$).

## 4. Discussion

Our results show that the amphipod community from the YCS is structured into three main species assemblages (Western Caribbean, Mid-Yucatan, and West-Yucatan) distributed along a longitudinal gradient and mainly responds to the bottom environmental and hydrography variabilities. The periodical presence of the upwelling system in the eastern sector of the YCS cause a marked temporal variability inside each of the detected assemblages. Furthermore, the species richness, abundance, and species composition for each assemblage were constrained by the depth gradient effects.

### *4.1. Amphipod species diversity*

The observed species richness (117 spp.) is so far the highest reported for benthic amphipods from any shelf subtidal habitats in the eastern and western sectors of the YCS (see Martín et al., 2013; Paz-Ríos

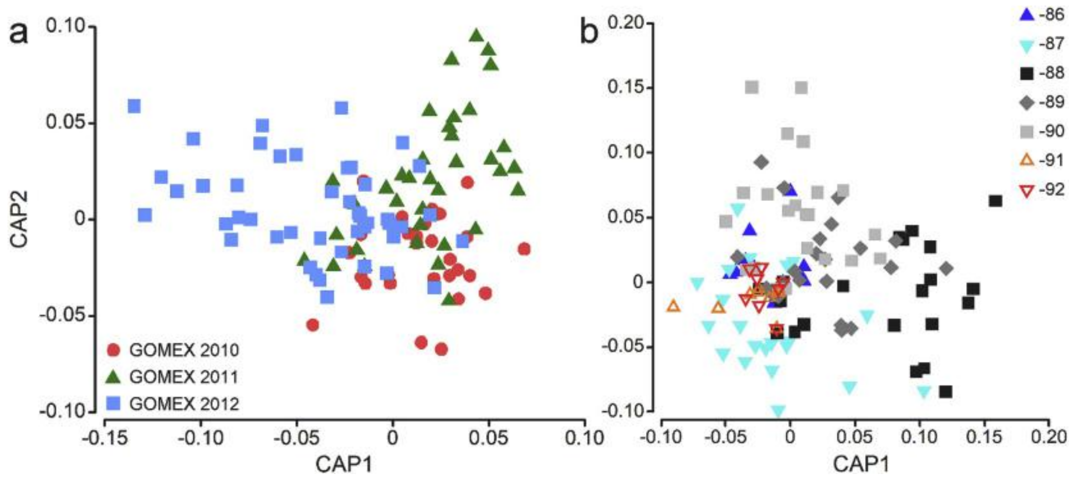


**Fig. 5.** Canonical analysis of principal coordinates (CAP) for the ordination of compositions and relative abundances of the amphipod community, as a function of the sampling year (a) and geographic longitude (b).

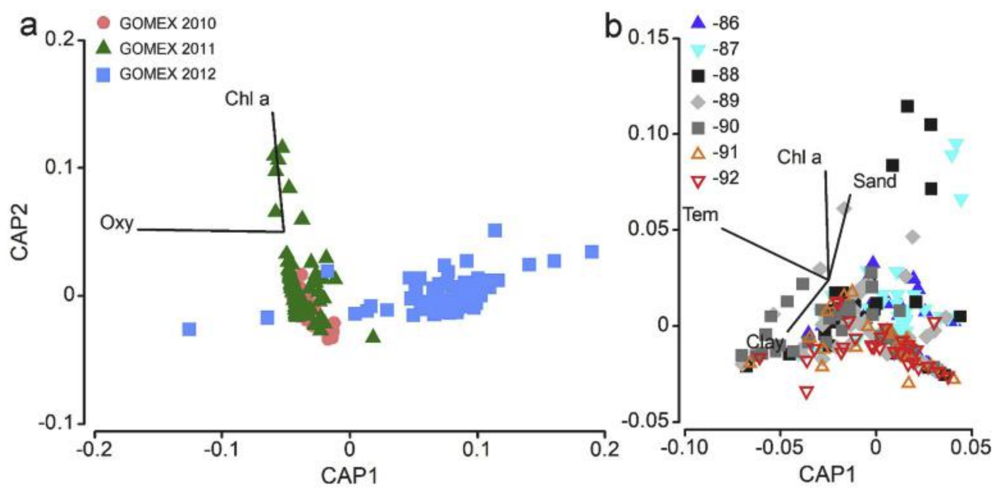


**Fig. 6.** Canonical analysis of principal coordinates (CAP) for the ordination of records in environmental variables, as a function of the sampling year (a) and geographic longitude (b). The deployed variables account for a Pearson's correlation of 0.5 in the ordination of sampling sites. Environmental variables: Chl a, chlorophyll-*a*; Oxy, dissolved oxygen; Tem, temperature.

**Table 4**
Range of bottom water variables and sediment characteristics by identified longitudinal geographic zone.

| | West-Yucatan | Mid-Yucatan | Western Caribbean |
|---|---|---|---|
| Temperature (°C) | 13.9–29.2 | 13.9–29.4 | 14.7–26.4 |
| Salinity (PSU) | 35.8–36.6 | 35.8–36.7 | 35.9–37.2 |
| Dissolved oxygen (ml $l^{-1}$) | 0.1–5.7 | 0.1–5.6 | 0.1–5.6 |
| Chlorophyll-*a* (mg $m^{-3}$) | 0.1–1 | 0.07–7.5 | 0.06–6.4 |
| Sand content (%) | 54–88.5 | 63.5–90 | 76.5–88.5 |
| Silt content (%) | 2–32 | 0–16 | 0–4 |
| Clay content (%) | 9.5–33 | 9.0–28.5 | 10.0–20.5 |
| Organic matter content (%) | 0.8–2.2 | 0.5–2.4 | 0.4–1.5 |

and Ardisson, 2013; Monroy-Velázquez et al., 2017). An incremental change in amphipod richness was observed from 2010 to 2012; however, despite an unprecedented sampling effort for benthic amphipods in the YCS, the estimated species accumulation curves suggest a high probability of obtaining at least 37% more species if different spatial and temporal scales in the sampling approach are used. The potential to obtain more amphipod species, represented here on the values of observed and estimated species richness, might imply that the species composition observed in the YCS forms part of a nested assemblage from another species pool regionally most diverse, e.g., ecoregion, province. The variability of the total species richness from 2010 to 2012 was probably associated with the major changes on the bottom environmental factors occurring at major temporal scales. Annually, assemblages subject to relatively similar environmental conditions (i.e., upwelling in 2010 and 2011) tended to be continuous and thus constants, and assemblages subject to different environmental conditions (i.e., upwelling in 2010 and 2011 versus non-upwelling in 2012) tended to be discontinuous and thus variables. Despite these contrasting scenarios, a general consistent pattern of three assemblages as a function of depth and longitudinal geographic zone was observed. A similar pattern, associated with the changes into the water and sediment characteristic was described in the YCS when all the benthic community was considered (Hernandez-Avila et al., 2020).

The observed change in sediment texture mostly composed by sand in the east to the incremental changes in clay contents to the west, might increase the diversity of soft-sediment habitats in the YCS contributing to the spatial variability of the amphipod richness, as was observed in other carbonate shelves (Poore et al., 2014; Ellis et al., 2017; Henkel and Politano, 2017). In the western YCS, amphipods associated with different grain size classes on subtidal habitats nearby coral reef systems

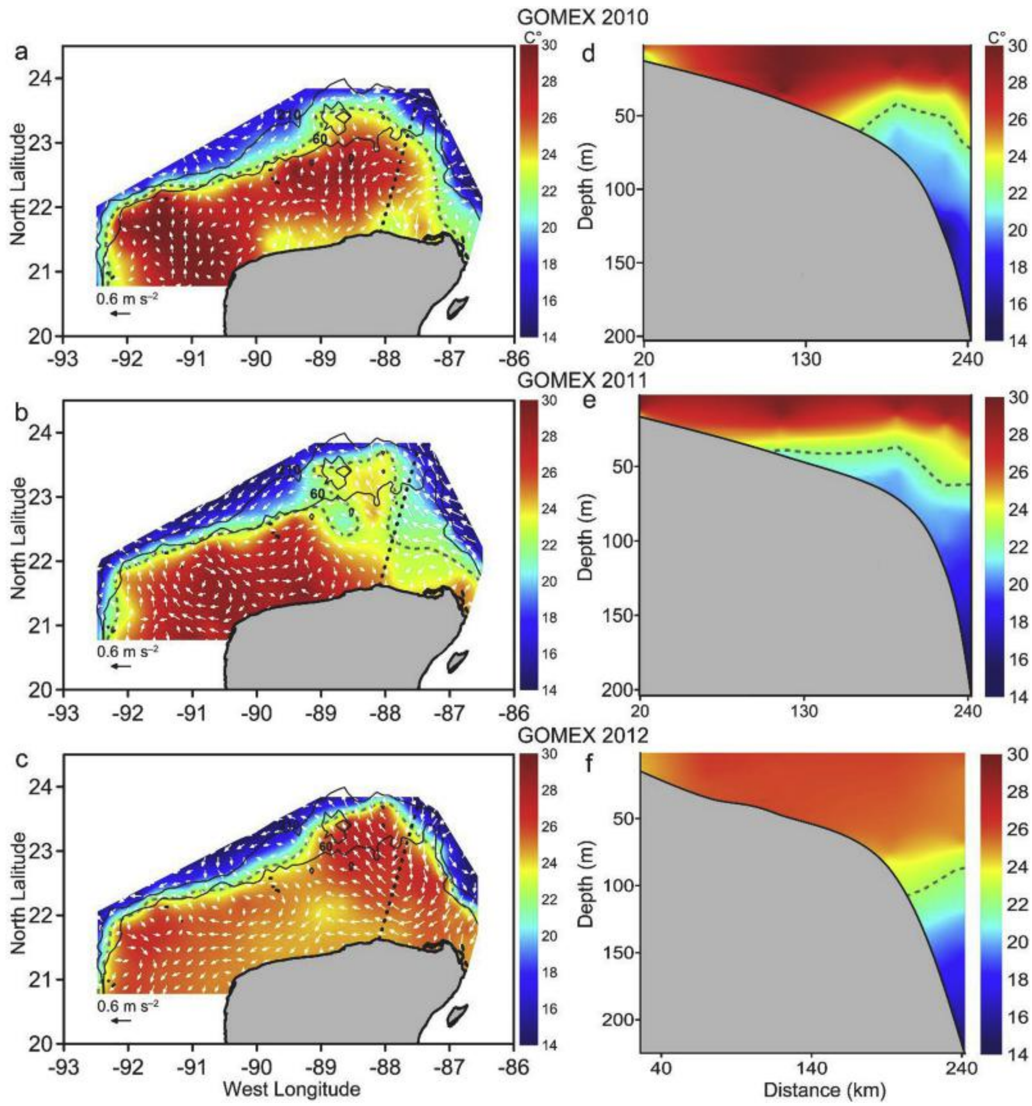


**Fig. 7.** Contour maps of the bottom-water temperature (a–c) and vertical profiles of temperature on one cross-shelf transect (d–f) per sampling year. Maps and profiles were interpolated using the ordinary Kriging method. Average values of surface current field (arrow vectors) for each cruise were obtained from satellite altimetry data (http://www.aoml.noaa.gov/phod/dhos/altimetry.php), combined with reanalysis data from the Ocean Circulation and Climate Advanced Modelling (OCCAM). GOMEX 2010 (11–21 September), GOMEX 2011 (23 September–3 October), GOMEX 2012 (27 November–8 December). The solid line represents the isobath for the upper limits of the inner (60 m) and outer shelf (210 m), the dashed line represents the isotherm of 22.5 °C, and the dotted line represents the cross-shelf transect.

were observed to be most diverse at the family category (Escobar-Briones and Jiménez-Guadarrama, 2010), evidencing the influence of sediment texture. Benthic amphipods can colonize different sediment textures (Wu and Shin, 1997), but the medium-fine sand sediments with low silt/clay content could enhances the establishment of higher amphipod abundance and diversity (Oakden, 1984; Marques and Bellan-Santini, 1993; Valério-Berardo et al., 2000). Indeed, our analyses detected a species turnover along the longitude gradient partially explained by change on the sediment texture, related with the sediment clay content, that contributed to the formation of the three different species assemblages studied here. The YCS geographic location, between the east border of the Southern Gulf of Mexico ecoregion and the adjacent Western Caribbean ecoregion (Spalding et al., 2007), could contributes to the relatively high species richness and species turnover due to the confluence of different biotic components of amphipods on the benthic habitats from those two ecoregions (Paz-Ríos and Ardisson, 2013). A recent analysis on regionalization of benthic macrofauna in the YCS outlines ecological boundaries similar those observed here, structured as discrete species assemblages, and suggesting soft-sediment habitats undergo spatial changes along the shelf that could enhance the environmental heterogeneity and contribute to increase the species richness (Hernandez-Avila et al., 2020).

### 4.2. *Spatiotemporal distribution patterns*

Changes in species richness, abundance, and species composition were significantly influenced by the longitudinal and depth gradients, demonstrating a heterogeneous distribution on the YCS. As expected, the depth gradient showed a significant influence on the amphipod community structure (Marques and Bellan-Santini, 1993; Jayaraj et al., 2008; Karenyi et al., 2018). In general, the amphipod composition in the outer shelf (60–210 m) showed the lowest values in richness and abundance along the entire YCS, as was observed for the macrofauna community (Hernandez-Avila et al., 2020). According to our analysis, the species composition and abundance of amphipods on the outer shelf was related with lower values for temperature and dissolved oxygen in the bottom water, as well for low organic matter and high clay content in the sediments. This relationship suggests a distribution trend consistent with the described for the macrofauna composition from the inner to outer Gulf of Mexico shelves that have been attributed to deeper waters, characterized as relatively stable and less heterogeneous soft-sediment habitats, with limited availability of food, uniform sediment texture, and high sediment oxygen consumption (Escobar-Briones and Falcon, 2005; Escobar-Briones et al., 2008; Wei et al., 2012). Our results suggest that the richness, abundance and community composition are responding to the changes of environment conditions and hydrographic variability of the YCS. The changes in bottom water and sediment

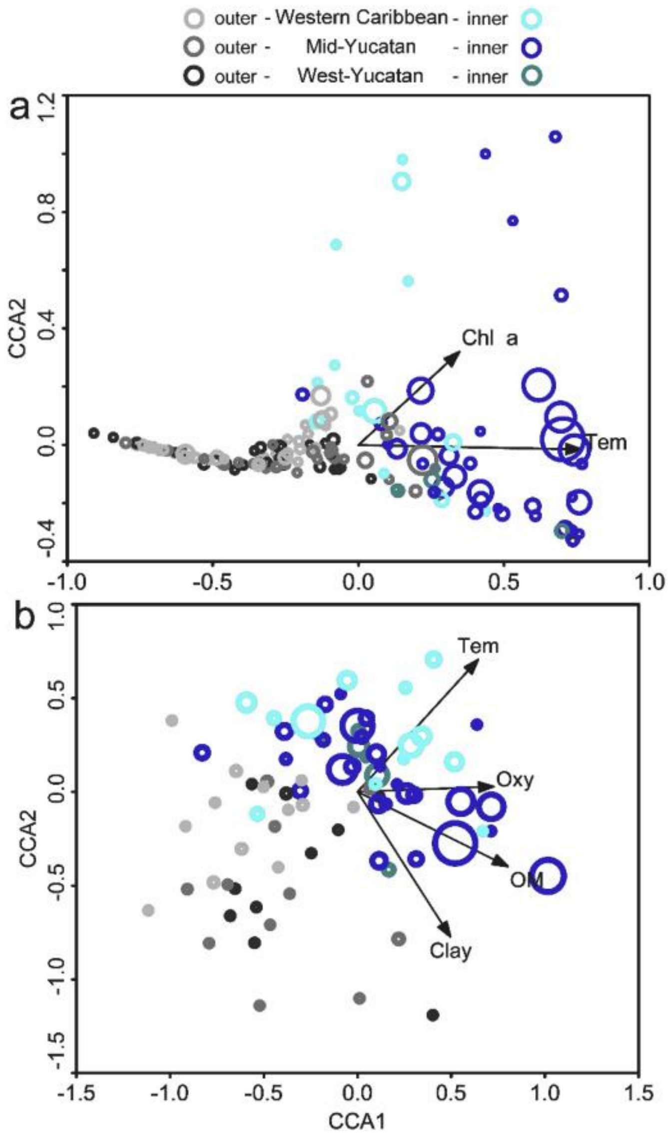


**Fig. 8.** Biplot projection of the canonical correspondence analysis (CCA) for a) 2010–2011 (significance of all canonical axes, $F = 2.758$, $p = 0.0001$) and b) 2012 (significance of all canonical axes, $F = 1.774$, $p = 0.0001$). Bubbles represent the total abundance, transformed into the fourth root. Environmental variables: Chl a, chlorophyll-*a*; OM, organic matter; Oxy, dissolved oxygen; Tem, temperature.

characteristics contributed to the formation of the three amphipod assemblages.

The higher values in species richness and abundance were observed at the inner shelf (<60 m), where amphipods undergone higher environmental variability, probably related to the diversity of benthic habitats occurring in the YCS (Paz-Ríos et al., 2019). Unimodal distribution trends for species richness and abundance were observed with higher values at the Mid-Yucatan assemblage, tending to decrease towards the West-Yucatan and Western Caribbean assemblages. A unimodal distribution is generally attributed to the influence of an environmental gradient on the species occurrence and abundance, which could suggest the suitability of benthic habitats along the gradient (Gray, 2002; Anderson, 2008). Our analysis suggests the existence of an environmental gradient related with sediment texture (clay content), temperature, and primary productivity along the geographical longitude that contributed to shape a nonlinear distribution in amphipod community characteristics. Here, the assemblage-environment relationship was described on the basis of hierarchically structured environmental gradients due to the combination of different variables acting as driving factors that shapes the macrofauna distribution (Zajac et al., 1998; Pitcher et al., 2012; Rodrigues and Pires-Vanin, 2012), as a function of geographic longitude.

The longitudinal environmental gradient is also supported by the documented influence of the dominant westward circulation in the YCS, which drives an important advective transport of materials and nutrients (Enriquez et al., 2010; Carrillo et al., 2017) that induces changes in the sedimentary environment (Balsam and Beeson, 2003; Appendini et al., 2012). The change in sediment characteristics, together with the oceanographic traits related to the main hydrographic circulation pattern (e.g., upwelling, anticyclonic eddy) will contribute to the unimodal distribution of amphipods, and to the formation of the three identified assemblages. The intra-annual variability of the ocean bottom environmental characteristics also induces spatiotemporal changes in the amphipod distribution and composition inside each observed assemblage, due to regional-scale seasonal hydrographic variations occurring in the YCS (Enriquez et al., 2010; Ruiz-Castillo et al., 2016). A recent study at the continental shelf of the southwestern Gulf of Mexico also shows that the seasonal hydrographic variations could cause marked spatiotemporal changes on the macrofauna community attributes and species composition (Salcedo et al., 2017). Our results show relatively similar environmental conditions between 2010 and 2011, contrasting with the different environmental characteristics in 2012. This same general bottom environmental pattern was observed on the amphipod community composition, suggesting that major changes on hydrographical condition, such as the upwelling phenomena would lead to major changes on amphipod species composition but not on the general community structure. The general conformation of the major assemblages remained without no significant changes. These findings imply a high ecological adaptability of benthic amphipods to hydrographic scenarios undergone on the YCS.

The difference in species richness and abundance from 2010–2011 to 2012 in the YCS may be explained by an adaptive response of amphipods to the environmental variability produced by dynamics of marine systems during annual cycles (Frid et al., 1996; Rodrigues and Pires-Vanin, 2012), as a large proportion of amphipods with few individuals were detected when an increment of species richness was observed. The incremental change of amphipod species richness and abundance observed in 2012 suggests a successional dynamic directed by disturbances on community distribution (Conlan, 1994; Wilson, 1994; Hewitt et al., 2016), associated with temporal changes in organic matter and regional hydrographic characteristics by the absence of an upwelling system.

The presence of the upwelling system seems to influence not only the ocean bottom water and sediment characteristics (e.g. organic matter content) of the east sector, where it occurs, but for all the YCS creating a gradient phenomenon from east to west. During 2010–2011, upwelling systems were observed where the West Caribbean assemblage occurs, due the intrusion of deeper cool water at the eastern inner shelf edge with an incremental change in primary production, measured as high chlorophyll-*a* concentrations (Reyes-Mendoza et al., 2016; Ruiz-Castillo et al., 2016). According to our results, the relatively low water temperature associated with the upwelling system may limit the species richness and abundance of benthic amphipods at the inner shelf, as has been shown in other continental shelves (Valério-Berardo et al., 2000; Quintana et al., 2015; Navarro-Barranco et al., 2017). Our results show lower abundance on the Western Caribbean assemblage and the Mid-Yucatan assemblage related with high chlorophyll-*a* concentrations and low bottom-water temperature. The influence of upwelling systems on the amphipod distribution persisted on the inner shelf until it reached the eastern area of the Mid-Yucatan assemblage, but in the west area of this same assemblage, away from the origin of the upwelling systems, a higher richness and abundance were observed as being related with the increment of bottom-water temperatures. On the other hand, our results suggest that the West-Yucatan assemblage was not influenced by upwelling systems, and the observed decreases in richness and abundance in this assemblage may be explained by a peninsula's edge effect at the west side of the shelf (Battisti, 2014).

The absence of an upwelling system in 2012 together with the presence of a warm-core anticyclonic eddy contributed to re-establishing the thermal exchange between water layers within the entire shelf (Reyes-Mendoza et al., 2016; Ruiz-Castillo et al., 2016). This hydrographic scenario, characterized by the increment of bottom-water temperatures at the inner shelf, probably favored the incremental change of abundances and species richness in the Western Caribbean and West-Yucatan assemblages. The amphipod life-cycle traits (e.g. high fecundity, parental care, low mobility) play a key role in their development as assemblages (Conlan, 1994), responding at community level to major hydrological phenomena such as the impact of changes on bottom water temperature (Highsmith and Coyle, 1991; Navarro-Barranco et al., 2017) and to sediment characteristics such as the grain size composition (Dernie et al., 2003; Hernández-Arana et al., 2003). Also, their direct development and local recruitment makes them a good indicator for year-to-year variations of the environmental conditions on the YCS, and the species with low abundances contribute to the temporal changes on the diversity patterns (Zajac et al., 1998; Ellingsen et al., 2007). In the absence of the upwelling system, the warm-core anticyclonic eddy (Salas-de-León et al., 2004; Cruz-Gómez et al., 2008) and the advective transport of the circulation over the YCS (Enriquez et al., 2010; Carrillo et al., 2017) may induce a vertical flux (downwelling circulation) of warm water and nutrients (Mahadevan et al., 2008; Durán-Campos et al., 2017), represented on our analyses by the higher concentrations of dissolved oxygen on the bottom-water and the sediment organic matter content. This scenario may favor a food input causing incremental changes in amphipod abundance and richness. The mixed water column by the active air-sea interaction and the absence of upwelling promotes a flux between benthic and pelagic components, and sets better conditions to the benthic macrofauna development, including amphipods (Soto and Escobar-Briones, 1995; Valério-Berardo et al., 2000; Quintana et al., 2015; Navarro-Barranco et al., 2017). The capacity of the amphipod community to respond to different hydrographic scenarios enhances its permanence in the YCS, which is a fundamental aspect for resilience in the context of broader environmental changes on benthic ecosystems.

## 5. Conclusion

Three different amphipod assemblages (Western Caribbean, Mid-Yucatan, and West-Yucatan) spatially structured along a longitude gradient were observed in the YCS, and were mainly influenced by the environmental conditions associated with the depth gradient and the hydrographic variability due to the temporary presence of an upwelling system. The presence of the upwelling system (2010–2011), characterized by high chlorophyll-*a* concentrations in the Western Caribbean and eastern Mid-Yucatan zones, may limit the establishment of high amphipod species richness and abundance, related with relatively lower bottom-water temperatures. The absence of upwelling (2012), together with the warm-core anticyclonic eddy, caused an increase in bottom-water temperatures throughout the entire shelf, which could favor the presence of higher concentrations of sediment organic matter content, that could cause incremental changes of species richness and abundance, mostly in the Mid-Yucatan zone. Our results show that despite the marked temporal hydrographic variability of the YCS, the spatial structure of the amphipod community remains stable shown a longitudinal geographic gradient. These findings suggest the hydrographic variability and sediment characteristics could be the main drivers that shapes the soft-sediment amphipod community distribution and diversity of the YCS.

## Declaration of competing interest

None.

## Acknowledgments

We thank Sara Balan and Anabel Leon (Laboratorio de Biodiversidad Marina y Cambio Climatico, El Colegio de la Frontera Sur) for collecting and preparing the amphipod samples, to Edlin Guerra Castro (Universidad Nacional Autonoma de Mexico) for advices on statistical analyses, and the anonymous reviewers for their value comments. We also thank the National Council of Science and Technology of Mexico (CONACYT) for the scholarship assigned to CEPR. The oceanographic campaigns were financed by the National Institute of Ecology and Climate Change, Mexico, according to the agreement SEMARNAT (Secretary for the Environment and Natural Resources, Mexico), No. 511.2/3596. Financial support to CEPR and DP was funded by the National Council of Science and Technology of Mexico - Mexican Ministry of Energy - Hydrocarbon Trust, project 201441. This is a contribution of the Gulf of Mexico Research Consortium (CIGoM).

## References

Anderson, M.J., 2008. Animal-sediment relationships re-visited: characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. J. Exp. Mar. Biol. Ecol. 366, 16–27. https://doi.org/10.1016/j.jembe.2008.07.006.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.

Appendini, C.M., Salles, P., Mendoza, E.T., López, J., Torres-Freyermuth, A., 2012. Longshore sediment transport on the northern coast of the Yucatan Peninsula. J. Coast Res. 28, 1404–1417. https://doi.org/10.2112/JCOASTRES-D-11-00162.1.

Arfianti, T., Costello, M.J., 2019. The biological, ecological, and ecosystem roles of marine Amphipoda. In: Reference Module in Earth Systems and Environmental Sciences, 2019, pp. 1–9. https://doi.org/10.1016/B978-0-12-409548-9.11800-7.

Balsam, W.L., Beeson, J.P., 2003. Sea-floor sediment distribution in the Gulf of Mexico. Deep Sea Res. Part I Oceanogr. Res. Pap. 50, 1421–1444. https://doi.org/10.1016/j.dsr.2003.06.001.

Battisti, C., 2014. Peninsular patterns in biological diversity: historical arrangement, methodological approaches and causal processes. J. Nat. Hist. 48, 2701–2732. https://doi.org/10.1080/00222933.2014.925599.

Bouyoucos, G.J., 1962. Hydrometer method improved for making particle size analyses of soils. Agron. J. 54, 464–465. https://doi.org/10.2134/agronj1962.00021962005400050028x.

Carrillo, L., Lamkin, J.T., Johns, E.M., Vásquez-Yeomans, L., Sosa-Cordero, F., Malca, E., Smith, R.H., Gerard, T., 2017. Linking oceanographic processes and marine resources in the western caribbean sea large marine ecosystem subarea. Environ. Dev. 22, 84–96. https://doi.org/10.1016/j.envdev.2017.01.004.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x.

Clarke, K.R., Gorley, R.N., 2016. PRIMER V7: User Manual/Tutorial. PRIMER-E, Plymouth.

Colwell, R.K., 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

Conlan, K.E., 1994. Amphipod crustaceans and environmental disturbance: a review. J. Nat. Hist. 28, 519–554. https://doi.org/10.1080/00222939400770241.

Constable, A.J., 1999. Ecology of benthic macro-invertebrates in soft-sediment environments: a review of progress towards quantitative models and predictions. Aust. J. Ecol. 24, 452–476. https://doi.org/10.1046/j.1442-9993.1999.00977.x.

Cruz-Gómez, R.C., Monreal-Gómez, M.A., Bulgakov, S.N., 2008. Efectos de los vórtices en sistemas acuáticos y su relación con la química, biología y geología. Interciencia 33, 741–746.

Dauvin, J.-C., Ruellet, T., 2007. Polychaete/amphipod ratio revisited. Mar. Pollut. Bull. 55, 215–224. https://doi.org/10.1016/j.marpolbul.2006.08.045.

Dauvin, J.-C., Thiébaut, E., Gomez Gesteira, J.L., Ghertsos, K., Gentil, F., Ropert, M., Sylvand, B., 2004. Spatial structure of a subtidal macrobenthic community in the Bay of Veys (western Bay of seine, English channel). J. Exp. Mar. Biol. Ecol. 307, 217–235. https://doi.org/10.1016/j.jembe.2004.02.005.

Demchenko, N.L., Chapman, J.W., Durkina, V.B., Fadeev, V.I., 2016. Life history and production of the western Gray Whale's prey, *Ampelisca eschrichtii* Krøyer, 1842 (Amphipoda, Ampeliscidae). PloS One 11, e0147304. https://doi.org/10.1371/journal.pone.0147304.

Dernie, K.M., Kaiser, M.J., Richardson, A.E., Warwick, R.M., 2003. Recovery of soft sediment communities and habitats following physical disturbance. J. Exp. Mar. Biol. Ecol. 285–286, 415–434. https://doi.org/10.1016/S0022-0981(02)00541-5.

Domínguez-Castanedo, N., Rojas-López, R., Solís-Weiss, V., Hernández-Alcántara, P., Granados-Barba, A., 2007. The use of higher taxa to assess the benthic conditions in the southern Gulf of Mexico. Mar. Ecol. 28, 161–168. https://doi.org/10.1111/j.1439-0485.2007.00178.x.

Durán-Campos, E., Salas-de-León, D.A., Monreal-Gómez, M.A., Coria-Monter, E., 2017. Patterns of chlorophyll-*a* distribution linked to mesoscale structures in two contrasting areas Campeche Canyon and Bank, Southern Gulf of Mexico. J. Sea Res. 123, 30–38. https://doi.org/10.1016/j.seares.2017.03.013.

Ellingsen, K.E., Hewitt, J.E., Thrush, S.F., 2007. Rare species, habitat diversity and functional redundancy in marine benthos. J. Sea Res. 58, 291–301. https://doi.org/10.1016/j.seares.2007.10.001.

Ellis, J., Anlauf, H., Kürten, S., Lozano-Cortés, D., Alsaffar, Z., Cúrdia, J., Jones, B., Carvalho, S., 2017. Cross shelf benthic biodiversity patterns in the Southern Red Sea. Sci. Rep. 7, 437. https://doi.org/10.1038/s41598-017-00507-y.

Enriquez, C., Mariño-Tapia, I., Herrera-Silveira, J., 2010. Dispersion in the Yucatan coastal zone: implications for red tide events. Continent. Shelf Res. 30, 127–137. https://doi.org/10.1016/j.csr.2009.10.005.

Enriquez, C., Mariño-Tapia, I., Jeronimo, G., Capurro-Filograsso, L., 2013. Thermohaline processes in a tropical coastal zone. Continent. Shelf Res. 69, 101–109. https://doi.org/10.1016/j.csr.2013.08.018.

Escobar-Briones, E., Falcon, L.I., 2005. Sediment oxygen consumption in the southwestern Gulf of Mexico. In: Barnes, P.W., Thomas, J.P. (Eds.), Benthic Habitats and the Effects of Fishing. American Fisheries Society, Bethesda, pp. 219–233.

Escobar-Briones, E., Jiménez-Guadarrama, E.L., 2010. Macrocrustáceos (Peracarida, Decapoda) de fondos carbonatados del sector Occidental del Banco de Campeche en el sur del Golfo de México. Rev. Mex. Biodivers. Supl. 81, S63–S72.

Escobar-Briones, E., Santillán, E.L.E., Legendre, P., 2008. Macrofaunal density and biomass in the campeche canyon, southwestern Gulf of Mexico. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 2679–2685. https://doi.org/10.1016/j.dsr2.2008.07.017.

Frid, C.L.J., Buchanan, J.B., Garwood, P.R., 1996. Variability and stability in benthos: twenty-two years of monitoring off Northumberland. ICES J. Mar. Sci. 53, 978–980.

Gaudette, H., Flight, W., Toner, L., Folger, D., 1974. An inexpensive tritation method for the determination of organic carbon in recent sediments. J. Sediment. Petrol. 44, 249–253. https://doi.org/10.1306/74D729D7-2B21-11D7-8648000102C1865D.

Gray, J.S., 2002. Species richness of marine soft sediments. Mar. Ecol. Prog. Ser. 244, 285–297.

Gómez-Gesteira, J.L., Dauvin, J.-C., 2000. Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. Mar. Pollut. Bull. 40, 1017–1027. https://doi.org/10.1016/S0025-326X(00)00046-1.

Henkel, S.K., Politano, K.K., 2017. Small proportions of silt linked to distinct and predictable differences in marine macrofaunal assemblages on the continental shelf of the Pacific Northwest. Continent. Shelf Res. 144, 38–49. https://doi.org/10.1016/j.csr.2017.06.016.

Hernández-Arana, H.A., Rowden, A.A., Attrill, M.J., Warwick, R.M., Gold-Bouchot, G., 2003. Large-scale environmental influence on the benthic macroinfauna of the southern Gulf of Mexico. Estuar. Coast Shelf Sci. 58, 825–841. https://doi.org/10.1016/S0272-7714(03)00188-4.

Hernandez-Avila, I., Ocaña, F.A., Pech, D., 2020. Testing marine regional-scale hypotheses along the Yucatan continental shelf using soft-bottom macrofauna. PeerJ 8, e8227. https://doi.org/10.7717/peerj.8227.

Hernández-Guevara, N.A., Pech, D., Ardisson, P.-L., 2008. Temporal trends in benthic macrofauna composition in response to seasonal variation in a tropical coastal lagoon, Celestun, Gulf of Mexico. Mar. Freshw. Res. 59, 772–779. https://doi.org/10.1071/MF07189.

Hewitt, J.E., Thrush, S.F., Halliday, J., Duffy, C., 2005. The importance of small-scale habitat structure for maintaining beta diversity. Ecology 86, 1619–1626. https://doi.org/10.1890/04-1099.

Hewitt, J.E., Thrush, S.F., Ellingsen, K.E., 2016. The role of time and species identities in spatial patterns of species richness and conservation. Conserv. Biol. 30, 1080–1088. https://doi.org/10.1111/cobi.12716.

Highsmith, R.C., Coyle, K.O., 1991. Amphipod life histories: community structure, impact of temperature on decoupled growth and maturation rates, productivity, and P:B ratios. Am. Zool. 31, 861–873. https://doi.org/10.1093/icb/31.6.861.

Jayaraj, K.A., Josia, J., Denesh Kumar, P.K., 2008. Infaunal macrobenthic community of soft bottom sediment in a tropical shelf. J. Coast Res. 24, 708–718. https://doi.org/10.2112/06-0790.1.

Johnson, W.S., Stevens, M., Watling, L., 2001. Reproduction and development of marine peracarideans. Adv. Mar. Biol. 39, 105–260.

Karenyi, N., Sink, K., Nel, R., Clark, A.E., Altwegg, R., 2018. Imperfect detection distorts depth-related trends in marine macrofaunal species richness. Ecography 41, 1698–1706. https://doi.org/10.1111/ecog.03439.

Kraufvelin, P., Perus, J., Bonsdorff, E., 2011. Scale-dependent distribution of soft-bottom infauna and possible structuring forces in low diversity systems. Mar. Ecol. Prog. Ser. 426, 13–28.

Link, J.S., Bolles, K., Milliken, C.G., 2002. The feeding ecology of flatfish in the Northwest Atlantic. J. Northwest Atl. Fish. Sci. 30, 1–17.

Logan, B.W., Harding, J.L., Aur, W.M., Williams, J.D., Sneat, R.G., 1969. Carbonate sediments on reefs, Yucatan shelf, Mexico, Part I, late quaternary sediments. Am. Assoc. Pet. Geol. Mem. 11, 7–128.

Mahadevan, A., Thomas, L.N., Tandon, A., 2008. Comment on "eddy/wind interactions stimulate extraordinary Mid-Ocean plankton blooms". Science 320, 448. https://doi.org/10.1126/science.1152111.

Marques, J.C., Bellan-Santini, D., 1993. Biodiversity in the ecosystem of the Portuguese continental shelf: distributional ecology and the role of benthic amphipods. Mar. Biol. 115, 555–564. https://doi.org/10.1007/BF00349362.

Marsden, I.D., Rainbow, P.S., 2004. Does the accumulation of trace metals in crustaceans affect their ecology—the amphipod example? J. Exp. Mar. Biol. Ecol. 300, 373–408. https://doi.org/10.1016/j.jembe.2003.12.009.

Martín, A., Díaz, Y., Miloslavich, P., Escobar-Briones, E., Guerra-García, J.M., Ortiz, M., Valencia, B., Giraldo, A., Klein, E., 2013. Regional diversity of Amphipoda in the caribbean sea. Rev. Biol. Trop. 61, 1681–1720.

Merino, M., 1997. Upwelling on the Yucatan shelf: hydrographic evidence. J. Mar. Syst. 13, 101–121. https://doi.org/10.1016/S0924-7963(96)00123-6.

Monroy-Velázquez, L.V., Rodríguez-Martínez, R.E., Alvarez, F., 2017. Taxonomic richness and abundance of cryptic peracarid crustaceans in the puerto morelos reef National park, Mexico. PeerJ 5, e3411. https://doi.org/10.7717/peerj.3411.

Navarro-Barranco, C., McNeill, C.L., Widdicombe, C.E., Guerra-García, J.M., Widdicombe, S., 2017. Long-term dynamics in a soft-bottom amphipod community and the influence of the pelagic environment. Mar. Environ. Res. 129, 133–146. https://doi.org/10.1016/j.marenvres.2017.04.013.

Oakden, J.M., 1984. Feeding and substrate preference in five species of phoxocephalid amphipods from central California. J. Crustac Biol. 4, 233–247.

Paz-Ríos, C.E., 2008. Distribución espacial de la comunidad de anfípodos gamáridos (Crustacea) al norte de la península de Yucatán, México. In: A, J., Sánchez, M.G., Hidalgo-Mihart, S.L., Arriaga-Weiss, W.M., Contreras-Sánchez (Eds.), Perspectivas en Zoología Mexicana. Fondo Editorial UJAT: Villahermosa, pp. 101–110.

Paz-Ríos, C.E., Ardisson, P.-L., 2013. Benthic amphipods (Amphipoda: gammaridea and Corophiidea) from the Mexican southeast sector of the Gulf of Mexico: checklist, new records and zoogeographic comments. Zootaxa 3635, 137–173. https://doi.org/10.11646/zootaxa.3635.2.4.

Paz-Ríos, C.E., Ardisson, P.-L., 2018. Intra-annual variability of a benthic amphipod assemblage (Crustacea: Amphipoda) in a tropical shallow coastal environment. Thalassas 34, 289–300. https://doi.org/10.1007/s41208-017-0063-9.

Paz-Ríos, C.E., Pech, D., 2019. *Gammaropsis elvirae* sp. nov., a widely distributed amphipod (Amphipoda: photidae) in the Yucatan Shelf, with ecological comments and a key for the genus in tropical America. Zootaxa 4555, 359–371. https://doi.org/10.11646/zootaxa.4555.3.5.

Paz-Ríos, C.E., Simões, N., Pech, D., 2019. Species richness and spatial distribution of benthic amphipods (Crustacea: peracarida) in the alacranes reef National park, Gulf of Mexico. Mar. Biodivers. 49, 673–682. https://doi.org/10.1007/s12526-017-0843-8.

Pech, D., Ardisson, P.-L., Hernández-Guevara, N.A., 2007. Benthic community response to habitat variation: a case of study from a natural protected area, the Celestun coastal lagoon. Continent. Shelf Res. 27, 2523–2533. https://doi.org/10.1016/j.csr.2007.06.017.

Pitcher, C.R., Lawton, P., Ellis, N., Smith, S.J., Incze, L.S., Wei, C.-L., Greenlaw, M.E., Wolff, N.H., Sameoto, J.A., Snelgrove, P.V.R., 2012. Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. J. Appl. Ecol. 49, 670–679. https://doi.org/10.1111/j.1365-2664.2012.02148.x.

Poore, G.C.B., Avery, L., Błażewicz-Paszkowycz, M., Browne, J., Bruce, N.L., Gerken, S., Glasby, C., Greaves, E., McCallum, A.W., Staples, D., Syme, A., Taylor, J., Walker-Smith, G., Warne, M., Watson, C., Williams, A., Wilson, R.S., Woolley, S., 2014. Invertebrate diversity of the unexplored marine western margin of Australia: taxonomy and implications for global biodiversity. Mar. Biodivers. 45, 271–286. https://doi.org/10.1007/s12526-014-0255-y.

Quintana, C.O., Bernardino, A.F., de Moraes, P.C., Valdemarsen, T., Sumida, P.Y.G., 2015. Effects of coastal upwelling on the structure of macrofaunal communities in SE Brazil. J. Mar. Syst. 143, 120–129. https://doi.org/10.1016/j.jmarsys.2014.11.003.

Reyes-Mendoza, O., Mariño-Tapia, I., Herrera-Silveira, J., Ruiz-Martínez, G., Enriquez, C., Largier, J.L., 2016. The effects of wind on upwelling off Cabo Catoche. J. Coast Res. 32, 638–650. https://doi.org/10.2112/JCOASTRES-D-15-00043.1.

Rodrigues, C.W., Pires-Vanin, A.M.S., 2012. Spatio-temporal and functional structure of the amphipod communities off Santos, Southwestern Atlantic. Braz. J. Oceanogr. 60, 421–439. https://doi.org/10.1590/S1679-87592012000300013.

Rodríguez-Pliego, P., Hernández-Arana, H.A., Ardisson, P.-L., 2011. Partitioning spatial and temporal variability of tropical near-shore macrobenthic assemblages affected by natural and anthropogenic disturbances. Mar. Freshw. Res. 62, 342–349. https://doi.org/10.1071/MF10165.

Ruiz-Castillo, E., Gomez-Valdes, J., Sheinbaum, J., Rioja-Nieto, R., 2016. Wind-driven coastal upwelling and westward circulation in the Yucatan shelf. Continent. Shelf Res. 118, 63–76. https://doi.org/10.1016/j.csr.2016.02.010.

Sainte-Marie, B., 1991. A review of the reproductive bionomics of aquatic gammaridean amphipods: variations of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223, 189–227. https://doi.org/10.1007/BF00047641.

Salas-de-León, D.A., Monreal-Gómez, M.A., Signoret, M., Aldeco, J., 2004. Anticyclonic-cyclonic eddies and their impact on near-surface chlorophyll stocks and oxygen supersaturation over the Campeche Canyon, Gulf of Mexico. J. Geophys. Res. Oceans 109, C05012. https://doi.org/10.1029/2002JC001614.

Salcedo, D.L., Soto, L.A., Estradas-Romero, A., Botello, A.V., 2017. Interannual variability of soft-bottom macrobenthic communities of the NW Gulf of Mexico in relationship to the Deepwater Horizon oil spill. Mar. Pollut. Bull. 114, 987–994. https://doi.org/10.1016/j.marpolbul.2016.11.031.

Santibañez-Aguascalientes, N.A., Borja, A., Kuk-Dzul, J.G., Montero-Muñoz, J.L., Ardisson, P.-L., 2018. Assessing benthic ecological status under impoverished faunal situations: a case study from the southern Gulf of Mexico. Ecol. Indicat. 91, 679–688. https://doi.org/10.1016/j.ecolind.2018.04.048.

Sanz-Lázaro, C., Marín, A., 2011. Diversity patterns of benthic macrofauna caused by marine fish farming. Diversity 3, 176–199. https://doi.org/10.3390/d3020176.

Soliman, Y.S., Rowe, G.T., 2008. Secondary production of *Ampelisca mississippiana* soliman and Wicksten, 2007 (Amphipoda, Crustacea) in the head of the Mississippi canyon, northern Gulf of Mexico. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 2692–2698. https://doi.org/10.1016/j.dsr2.2008.07.019.

Soto, L.A., Escobar-Briones, E., 1995. Coupling mechanisms related to trophic benthic production in the SW Gulf of Mexico. In: Eleftheriou, A., Ansell, A.D., Smith, C.J. (Eds.), 28th European Marine Biology Symposium. Institute of Marine Biology of Crete: Fredensborg, pp. 233–242.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the World: a bioregionalization of coast and shelf areas. Bioscience 57, 573–583. https://doi.org/10.1641/B570707.

ter Braak, C.J.K., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca.

Tunnell Jr., J.W., Chavez, E.A., Withers, K., 2007. Coral Reefs of the Southern Gulf of Mexico. Texas A&M University Press, Corpus Christi.

Valério-Berardo, M.T., Flynn, M.N., Wakabara, Y., 2000. Structure and dynamic of a shelf amphipod taxocoenosis in southeastern Brazil. Bull. Mar. Sci. 66, 59–72.

Wei, C.-L., Rowe, G.T., Escobar-Briones, E., Nunnally, C., Soliman, Y., Ellis, N., 2012. Standing stocks and body size of deep-sea macrofauna: predicting the baseline of 2010 *Deepwater Horizon* oil spill in the northern Gulf of Mexico. Deep-Sea Res. Part I Oceanogr. Res. Pap. 69, 82–99. https://doi.org/10.1016/j.dsr.2012.07.008.

Wilson, J.B., 1994. The 'intermediate disturbance hypothesis' of species coexistence is based on patch dynamics. N. Z. J. Ecol. 18, 176–181.

Williams, A., Althaus, F., Dunstan, P.K., Poore, G.C., Bax, N.J., Kloser, R.J., McEnnulty, F. R., 2010. Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100–1100 m depths). Mar. Ecol. 31, 222–236. https://doi.org/10.1111/j.1439-0485.2009.00355.x.

Williams, J.D., 1963. The Petrology and Petrography of Sediments from the Sigsbee Blanket, Yucatan Shelf. Mexico. Texas A & M University, Texas.

Wu, R.S.S., Shin, P.K.S., 1997. Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. Mar. Biol. 128, 475–487. https://doi.org/10.1007/s002270050114.

Zajac, R.N., Vozarik, J.M., Gibbons, B.R., 2013. Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscape structure. PloS One 8, e65823. https://doi.org/10.1371/journal.pone.0065823.

Zajac, R.N., Whitlatch, R.B., Thrush, S.F., 1998. Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. Hydrobiologia 375/376, 227–240. https://doi.org/10.1023/A:1017032200173.

Zavala-Hidalgo, J., Parés-Sierra, A., Ochoa, J., 2002. Seasonal variability of the temperature and heat fluxes in the Gulf of Mexico. Atmósfera 15, 81–104.