UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE CIENCIAS DEL MAR Y LIMNOLOGÍA

COMPOSICIÓN ESTRUCTURA Y DISTRIBUCIÓN DE LAS COMUNIDADES DE POLYCHAETA, PERACARIDA Y APLACOPHORA DE LA MACROFAUNA BENTÓNICA DEL MAR PROFUNDO DEL SUROESTE DEL GOLFO DE MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

M. en C. Octavio Quintanar Retama

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CIUDAD UNIVERSITARIA, CDMX. AGOSTO DE 2023.

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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
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ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión del Comité de Posgrado en Ciencias Biológicas, celebrada el día **08 de mayo de 2023** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **QUINTANAR RETAMA OCTAVIO** con número de cuenta **98552180** con la tesis titulada: **“Composición estructura y distribución de las comunidades de Polychaeta, Peracarida y Aplacophora de la macrofauna bentónica del mar profundo del suroeste del Golfo de México.”,** realizada bajo la dirección del **DR. ADOLFO GRACIA GASCA:**

Presidente: **DR. JOSÉ ESTUARDO LÓPEZ VERA**
Vocal: **DRA. MARÍA ADELA MONREAL GÓMEZ**
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Vocal: **DR. SERGIO IGNACIO SALAZAR VALLEJO**
Secretario: **DR. SERGIO CHÁZARO OLVERA**

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
“POR MI RAZA HABLARÁ EL ESPÍRITU”
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COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

c. c. p. Expediente del alumno

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Contenido

Resumen

Los patrones de diversidad y distribución de las comunidades de macrofauna bentónica en aguas profundas mexicanas del Golfo de México son poco conocidos en comparación con el norte del Golfo. Este estudio fue diseñado para contribuir al conocimiento de las comunidades de macrofauna a través de (i) evaluar su composición taxonómica a nivel de grandes grupos (filos, clases, subclases, superórdenes, órdenes) y a nivel de familia de tres de sus principales componentes: anélidos poliquetos, crustáceos peracáridos y moluscos aplacóforos y (ii) analizar sus patrones de distribución espacial en aguas profundas del suroeste del Golfo de México. El presente estudio se realizó en una amplia área geográfica (92,67°–96,70°O 18,74°–23,04°N) y gradiente batimétrico (185-3762 m de profundidad). Las muestras se recolectaron a bordo del B/O Justo Sierra (Universidad Nacional Autónoma de México) utilizando un box corer tipo Reineck durante los cruceros oceanográficos SOGOM 1-4 realizados del 3 al 27 de junio de 2015, del 31 de agosto al 20 de septiembre de 2016, del 21 de abril al 15 de mayo de 2017, y del 29 de agosto al 20 de septiembre de 2018, respectivamente. Se midieron trece parámetros ambientales (entre ellos: profundidad, salinidad, temperatura, oxígeno disuelto, tamaño de grano del sedimento, contenido de hidrocarburos y de materia orgánica en sedimentos). Para el análisis de datos, los sitios de muestreo se organizaron en tres categorías de profundidad (DC por sus siglas en inglés): zona batial superior (UBZ por sus siglas en inglés) (185–1500 m), zona batial inferior (LBZ por sus siglas en inglés) (1501–3000 m) y zona abisal (AZ por sus siglas en inglés) (3001–3762 m). Ambientalmente, la UBZ se caracterizó como una región con importantes variaciones en los valores de oxígeno disuelto, salinidad y temperatura. Además de altas concentraciones de materia orgánica y limo, bajos valores de carbonato y arcilla en sedimentos y altos valores de hidrocarburos aromáticos. Mientras que las regiones LBZ y AZ se distinguieron por una alta estabilidad en los valores de oxígeno disuelto, salinidad y temperatura, bajo contenido de materia orgánica y limo, altos valores de carbonato y arcilla e hidrocarburos aromáticos relativamente más bajos en los sedimentos. Se registraron 25 grandes grupos de la macrofauna; dos clases y cuatro familias de aplacóforos; 4 órdenes y 53 familias de peracáridos y 45 familias y 69 géneros de poliquetos. Las comunidades de macrofauna estuvieron dominadas por los poliquetos. Dentro de ellos, las familias dominantes fueron Spionidae, Paraonidae y Capitellidae y los géneros más abundantes: *Levinsenia*, *Prionospio* y *Paraprionospio*. El orden dominante en abundancia de los peracáridos fue Amphipoda seguido de Tanaidacea (36.4 % y 35.8 % de la abundancia total de peracáridos, respectivamente). En términos de diversidad Amphipoda registró el mayor número de familias (19) seguido de Isopoda (17). Las cinco familias dominantes dentro de los peracáridos fueron: Apseudidae, Phoxocephalidae, Caprellidae, Desmosomatidae y Nototanaidae. De moluscos aplacóforos registramos las dos clases: Solenogastres y Caudofoveata. De estos últimos, se registraron tres familias: Prochaetodermatidae, Chaetodermatidae y Limifossoridae. El taxón más abundante dentro de Aplacophora fue la familia Prochaetodermatidae (48% de la abundancia total). De manera general, las mayores abundancias de la macrofauna se registraron en sitios de menor profundidad cercanos a la línea de costa en la región sur del área de estudio, además de la zona de domos salinos de la Bahía de Campeche. Algunos sitios de la región noroeste frente a las costas del norte de Veracruz y de Tamaulipas también registraron valores intermedios y altos de abundancia. Los valores más bajos de abundancia se registraron en los sitios ubicados en la planicie abisal de Sigsbee. Batimétricamente, la comunidad en general y los poliquetos en particular registraron los valores más altos de diversidad en sitios de LBZ. Los peracáridos presentaron un patrón decreciente en los valores de diversidad de UBZ a AZ. En aplacóforos los valores más altos de abundancia y diversidad se registraron en UBZ. Se documentaron cambios en la estructura de la comunidad de macrofauna en general, de los poliquetos y los peracáridos asociados a cambios en la profundidad. Los principales estructuradores ambientales de las comunidades de macrofauna variaron en función del taxón en estudio. Para la macrofauna en general, el oxígeno disuelto, los hidrocarburos aromáticos, la materia orgánica y la profundidad fueron las variables más relacionadas con la distribución de la fauna. En el caso de los poliquetos: temperatura, tamaño de grano de sedimento y oxígeno disuelto. Para peracáridos: latitud, profundidad, temperatura e hidrocarburos alifáticos. Finalmente, para los aplacóforos: profundidad, temperatura y tamaño de grano de sedimento fueron las variables ambientales con valor más alto de correlación con la distribución faunística. Este estudio llena un vacío en el conocimiento de la diversidad y distribución de las comunidades de macrofauna bentónica de los fondos marinos profundos de una amplia área que cubre todo el rango batimétrico del sur del Golfo de México y proporciona una línea de base útil para comparar con áreas contaminadas y para evaluar el impacto de contaminación crónica y/o posibles accidentes por derrames de petróleo.

Abstract

The diversity and distribution patterns of benthic macrofauna communities in the deep seabed of the Mexican waters of the Gulf of Mexico are poorly known compared to the northern Gulf. This study was designed to contribute to the knowledge of macrofauna communities through (i) evaluating their taxonomic composition at the major taxa level (phyla, classes, subclasses, superorders, orders) and at the family level of three of its main components: polychaete annelids, peracarid crustaceans and aplacophoran mollusks and (ii) analyze their spatial distribution patterns in deep waters of the southwestern Gulf of Mexico. The composition of the benthic macrofauna was analyzed in a large geographical area (92.67°–96.70°W 18.74°–23.04°N) and wide bathymetric gradient (185-3762 m depth). Samples were collected on board the R/V Justo Sierra (Universidad Nacional Autónoma de México) using a Reineck type box corer during the SOGOM 1-4 oceanographic cruises carried out 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, respectively. Thirteen environmental parameters were measured (among them: depth, salinity, temperature, dissolved oxygen, sediment grain size, hydrocarbon, and organic matter content in sediments). For data analysis, sampling sites were organized into three depth categories (DC): upper bathyal zone (UBZ,185–1500 m), lower bathyal zone (LBZ,1501–3000 m) and abyssal zone (AZ,3001–3762 m). Environmentally, the UBZ was characterized as a region with significant variations in dissolved oxygen, salinity, and temperature values. In addition to high concentrations of organic matter and silt, low values of carbonate and clay in sediments and high values of aromatic hydrocarbons. Whereas the LBZ and AZ regions were distinguished by high dissolved oxygen, salinity, and temperature stability, low organic matter and silt content, high carbonate and clay values, and relatively lower aromatic hydrocarbons in the sediments. Twenty-five macrofauna high level taxa were recorded; two classes and four families of aplacophorans; 4 orders and 53 families of peracarids and 45 families and 69 genera of polychaetes.

The macrofauna communities were dominated by polychaetes. Among them, the dominant families were Spionidae, Paraonidae and Capitellidae and the most abundant genera were: *Levinsenia*, *Prionospio* and *Paraprionospio*. The dominant peracarid order in term of abundance was Amphipoda followed by Tanaidacea (36.4 % and 35.8 % of the total peracarids abundance, respectively). The five dominant families among the peracarids were: Apseudidae, Phoxocephalidae, Caprellidae, Desmosomatidae and Nototanaidae. Aplacophorous mollusks recorded two classes: Solenogastres and Caudofoveata. Of the latter, three families were registered: Prochaetodermatidae, Chaetodermatidae and Limifossoridae. The most abundant taxon among Aplacophora was the family Prochaetodermatidae (48% of the total abundance). In general, the highest macrofauna abundance values were recorded in shallow sites close to the coastline in the southern region of the study area, as well as the saline dome zone of the Campeche Bay. Some sites in the northwestern region in front of the Veracruz and Tamaulipas coasts also recorded intermediate and high values of abundance. The lowest abundance values were recorded in the sites located in the Sigsbee abyssal plain. The community in general and the polychaetes in particular registered the highest diversity values in LBZ sites. The peracarids presented a decreasing pattern from UBZ to AZ in the diversity values. In aplacophorans the highest values of abundance and diversity were recorded in UBZ. We documented depth-related changes in the structure of the high level macrofauna taxa community, of polychaetes and peracarids. The main environmental drivers of macrofauna communities varied depending on the target taxon. For the high level taxa, dissolved oxygen, aromatic hydrocarbons, organic matter and depth were the variables most related to the fauna distribution. In the case of polychaetes, temperature, sediment grain size and dissolved oxygen were the most important. For peracarids: latitude, depth, temperature and aliphatic hydrocarbons. Finally, for aplacophorans: depth, temperature, and sediment grain size were the environmental variables that presented the highest correlation with faunal distribution. This study fills a gap in the knowledge of the diversity and distribution of deep seabed benthic macrofaunal communities over a wide area that covers the entire bathymetric range of the southern Gulf of Mexico and provides a useful baseline for comparison with contaminated areas and for assessing the impact of chronic contamination and/or potential oil spill accidents.

La presente tesis cumple con el formato requerido por el Posgrado en Ciencias Biológicas de la UNAM para la obtención de grado a través tesis por artículos científicos. Por esta razón la organización de la tesis comprende un resumen, un abstract, una introducción general en español, los artículos publicados, los manuscritos generados, el artículo requisito y finalmente discusión y conclusiones generales en español.

Introducción

El 71 % de nuestro planeta está cubierto por los océanos (Tyler et al., 2016). De este sistema, el 90 % presenta una profundidad mayor a 200 m lo cual es considerado mar profundo (Fiege et al., 2010; Gage, 2001) con condiciones de falta de luz, alta presión hidrostática y baja temperatura. Además, es escasa e intermitente la disponibilidad de alimento por lo que existe una dependencia del aporte de materia orgánica (MO) producida en capas superficiales o en la región continental (Danovaro et al., 2014; Gage and Tyler, 1991). Las comunidades que habitan zonas de infiltraciones frías y de ventilas hidrotermales constituyen una excepción en cuanto a la dependencia de este aporte debido a que se sustentan en la producción primaria quimiosintética de algunas bacterias (Demopoulos et al., 2014). De tal manera que el mar profundo es el ecosistema más grande de la tierra. En este ambiente, el sustrato, está compuesto en su mayoría por sedimentos blandos (Gray, 2002) y alberga una alta diversidad, mucha de la cual es desconocida. Además, se han encontrado recursos explotables y se ha entendido el papel que juega como sumidero de CO2 resultado de la actividad humana (Danovaro et al., 2014; Group, 1994).

Lo anterior implica que las comunidades de macrofauna bentónica defondos suaves de mar profundo constituyan uno de los conjuntos faunísticos más grandesdel planeta en términos de área cubierta (Snelgrove, 1998). Estas comunidades están integradas por metazoos de menos de 1.5 cm de longitud que son retenidos en un tamiz con luz de malla de entre 250 y 500 µm (Gage, 2001; Hessler and Jumars, 1974; Rex, 1981; Rex et al., 2006). Esta fauna se caracteriza por ser capaz de moverse sobre un fondo blando como un medio continuo y de mover los granos de sedimento (generan bioturbación) (Duport et al., 2007; Kristensen et al., 2012; Valdemarsen et al., 2018). Por lo general, una docena de filos son los más frecuentes (Grassle, 1991). Los poliquetos, peracáridos y moluscos destacan por su importancia en términos de abundancia y diversidad (Brandt et al., 2018; Grassle and Maciolek, 1992). Los poliquetos llegan a representar entre la mitad y tres cuartas partes de la abundancia total (Glover et al., 2008;Jumars, 1975; Levin and Gooday, 2003; Qu et al., 2016) seguidos por crustáceos peracáridos y después por moluscos (Gage, 2001; Levin and Gooday, 2003; Rex et al., 2006). De tal manera que, estos tres grupos, llegan a constituir entre el 60 % y el 92 % deltotal de la abundancia de macrofauna bentónica (Bourque et al., 2017; Brandt et al., 2018;Galéron et al., 2009).

Los organismos de las comunidades de macrofauna bentónica de mar profundo suelen tener tamaño similar, se registran en bajas densidades y con una alta riqueza (Danovaro et al., 2014; Gage, 2001; Hargrave and Thiel, 1983). Es muy común registrar un solo ejemplar de cada especie, es decir, raramente se observa una dominancia (Gage, 2001; Hargrave and Thiel, 1983). De manera general, se sabe que la abundancia disminuye al aumentar la profundidad. Este patrón ha sido ampliamente documentado en el mar profundo (Baldrighi et al., 2014; Bernardino et al., 2016; Gage and Tyler, 1991; Hessler and Sanders, 1967), en el norte del Golfo de México (Wei et al., 2012a) y dentro del área de estudio (Escobar-Briones et al., 1999) y ha sido explicado por la disminución en la disponibilidad de materia orgánica con la profundidad (Morse and Beazley, 2008) y la distancia a la costa (Escobar-Briones and García-Villalobos, 2009) ya que el contenido de MO está relacionado con la abundancia de la infauna (Morse and Beazley, 2008; Wei et al., 2010b). Sin embargo, también se han reportado otras tendencias, comúnmente en estudios basados en el análisis de transectos (p. ej. Pérez-Mendoza et al., 2003). Estos cambios suelen asociarse con variaciones horizontales de algunos factores abióticos. Por otro lado, la diversidad en mar profundo exhibe frecuentemente un patrón batimétrico con valores más bajos en las regiones batial superior y abisal y más altos en profundidades intermedias (Ramirez-Llodra et al., 2010; Rex, 1981; Wei and Rowe, 2019).

Algunos autores sostienen que la mayor diversidad en esta región obedece a la mezcla de faunas entre las regiones batial y abisal (Levin et al., 2001; Snelgrove and Smith, 2002). Este patrón también puede variar en función del grupo en estudio, por ejemplo, los peracáridossuelen presentar una mayor diversidad en la región superior batial y esta disminuye al aumentar la profundidad (Golovan et al., 2013). Asimismo, se sabe que el tamaño de los organismos disminuye conforme aumenta la profundidad, aunque también se ha registrado gigantismo en este ambiente en taxones como Isopoda, Amphipoda y Picnogonida (Danovaro et al., 2014). Algunos autores sostienen que la disminución de tamaño con el aumento de la profundidad también es debida a la poca disponibilidad de alimento (Mengerink et al., 2014). Esta disminución de tamaño en zonas de mayor profundidad implica que los taxones que en zonas someras pertenecen claramente a la macrofauna, en zonas profundas suelen tener el tamaño de lo que se define como meiofauna en la primera. Esto sucede particularmente con los juveniles (Gage, 2001). De tal forma que la frontera entre estas categorías es abierta.

El concepto de macrofauna *sensu lato* implica toda la fauna recolectada en un tamiz de entre 250 y 500 micras, independientemente del grupo al que pertenezcan (Hessler and Jumars, 1974). Mientras que, la macrofauna *sensu stricto* no considera tres taxones que son componentes típicos de la meiofauna: Nematoda, Harpacticoida y Ostracoda

(Flach et al., 1999; Gage et al., 2002; Hessler and Jumars, 1974; Sibuet et al., 1989; Wei et al., 2012a). Este trabajo lodesarrollamos en el marco del concepto de macrofauna *sensu lato*.

Son diversos los factores estructuradores de estas comunidades, entre ellos, el tamaño de grano de sedimento, la disponibilidad de oxígeno (Etter and Grassle, 1992; Levin et al., 2001), el flujo de carbón orgánico (Hernández-Ávila et al., 2021) y la proximidad a la costa (Woolley et al., 2016). De acuerdo con Gage, (2001) del borde de la plataforma continental hasta los 1200 m de profundidad, el más importante de ellos es el sistema de corrientes de fondo. Una corriente mayor a 1 cm por segundo es capaz de resuspender el sedimento e impedir el establecimiento de organismos detritívoros y favorecer el establecimiento de filtradores. A mayores profundidades es más importante la influencia biogénica, particularmente la bioturbación. Los procesos de perturbación, seguidos de procesos sucesionales, también son fundamentales en la composición y estructuración de estas comunidades.

Las comunidades de macrofauna bentónica de mar profundo participan en los procesos de producción secundaria, bioturbación y bioirrigación de sedimentos (Snelgrove, 1998; Zhang et al., 2010), contribuyendo al transporte, enterramiento y absorción de contaminantes (Banta and Andersen, 2003; Snelgrove, 1998). Los contaminantes que son ingeridos por los organismos pueden bioacumularse y por lo tanto podrían afectar cadenas alimentarias completas (Somero, 1992). Además, participan en el proceso de sumidero de MO y transporte de oxígeno a las capas del subsuelo (Crawshaw et al., 2019) promoviendo la actividad bacteriana (Parkes et al., 1994). Además, afectan el transporte de sedimentos a través del aumento de la susceptibilidad del sistema a la erosión (Grant et al., 1982), y también pueden modificar los sedimentos finos alimentándolos y transformándolos en gránulos defecados más grandes, aumentando así la porosidad de los fondos blandos. Por lo tanto, la contribución de estas comunidades en los ciclos biogeoquímicos a través del reciclaje de nutrientes, las interacciones ecológicas y la transformación del medio ambiente es fundamental para sostener las profundidades marinas y el ecosistema oceánico global. Además, son muy útiles como indicadores de la salud ambiental bentónica debido a la baja movilidad y tolerancia o sensibilidad de algunas especies a los estresores ambientales (p.ej. hipoxia, contaminación y biorturbación) (Dean H. K., 2008; Guerra-García and García-Gómez, 2004).

El Golfo de México (GoM) representa un sistema de enorme importancia ecológica y económica para México. Las pesquerías, el turismo y la extracción de hidrocarburos son de las principales actividades económicas de la región. Sin embargo, la interacción entre las zonas someras y las zonas de mar profundo son escasamente entendidas. Una de las razones por la que no se cuenta con esta información es que el muestreo en mar profundo es muy costoso. Aún menos son los estudios que realizan un muestreo sistemático en diferentes temporadas (Reuscher and Shirley, 2017). De acuerdo con Qu et al., (2016), la distribución de las comunidades bentónicas en las profundidades marinas del GoM es bastante conocida y es posible predecir la abundancia, composición de especies y biodiversidad dependiendo de la localidad y la profundidad. Se han realizado varios estudios en el norte del GoM (Baguley et al., 2006a, 2006b; Carvalho et al., 2013; Pequegnat et al., 1990; Rowe et al., 1974; Sharma et al., 2011; Wei et al., 2012a, 2012b, 2010a, 2010b) que respaldan esta afirmación, sin embargo, existen pocos estudios sobre comunidades de macrofauna de aguas profundas en la Zona Económica Exclusiva de México (p. ej. Escobar-Briones et al., 1999; Hernández-Ávila et al., 2021; Pérez-Mendoza et al., 2003; Rowe and Menzel, 1971; Salcedo et al., 2017). Por lo tanto, la diversidad y distribución de las comunidades de macrofauna en los fondos marinos profundos de las aguas mexicanas del GoM son poco conocidas en comparación con el norte del GoM. Recientemente, existe un renovado interés por estudiar el GoM y tener un conocimiento integral de todo el Gran Ecosistema y sus respuestas a diferentes factores de estrés. Entre ellos, derrames de petróleo como los dos mega derrames de petróleo ocurridos en el GoM (Ixtoc 1, 1979-1980 y DHW, 2010). Eventos de esta magnitud podrían repetirse y son de gran preocupación debido a los impactos en el ecosistema de aguas profundas (Murawski et al., 2020; Pulster et al., 2020; Reuscher et al., 2020; Schwing et al., 2020).

Este estudio fue diseñado para contribuir al conocimiento de las comunidades de macrofauna a través de (i) evaluar la composición taxonómica de las comunidades de macrofauna a nivel de los principales taxones y a nivel de familia de tres de sus principales componentes: anélidos poliquetos, crustáceos peracáridos y moluscos aplacóforos y (ii) analizar sus patrones de distribución espacial en las profundidades marinas del suroeste del GoM. Los datos obtenidos del amplio rango batimétrico y geográfico cubierto en el sur del GoM contribuirán sustancialmente al conocimiento de las comunidades de macrofauna en esta pobre área estudiada proporcionando información única para comprender el GoM como un ecosistema completo.

Además, proporcionará datos de referencia que podrían ser útiles para evaluar el impacto de las actividades impulsadas por el hombre, como derrames accidentales de petróleo y/o cambios en el ecosistema a largo plazo.

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Data Article

Polychaete dataset of the southwestern Gulf of Mexico including: taxonomic checklist, abundance, bathymetric distribution, functional diversity, geographic location, and sampling sites depth

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ABSTRACT

A taxonomic list of 69 genera belonging to 33 families of the Polychaeta class (Annelida) collected in 54 deepwater sites of the southwestern Gulf of Mexico is presented. Abundance data of these 69 genera is also included. A dataset of geographical location and depth of sampling sites is given. Graphs of depth related community functional diversity variation are shown. The biological material was obtained from sediment samples collected aboard the Justo Sierra Oceanographic Vessel of the National Autonomous University of Mexico using a Reineck-type box corer with an effective area of 0.16 m^2. In each core a subsample of 0.08 m^2 and 13 cm deep was taken and washed through a 500-micron sieve with filtered seawater. Abundances were standardized to individuals per square meter. The average abundance contribution percentage graphs were done calculating the average standardized abundance of each guild and the contribution

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percentage of each one to the four depth categories established: Upper bathyal zone (UBZ); middle bathyal zone (MBZ); lower bathyal zone (LBZ) and abyssal zone (ABYZ). These data could be useful for comparative purposes with new data of polychaete communities in the same area or another region.

Specifications Table

Subject	Biological Sciences (Biodiversity)
Specific subject area	This dataset provides information about the polychaete biodiversity and ecology of the southwestern deep sea of the Gulf of Mexico.
Type of data	Table Figure
How the data were acquired	The biological material was obtained in two cruises carried out on board the Oceanographic Vessel Justo Sierra of the National Autonomous University of Mexico. The samples were collected using a Reineck-type box corer with an effective area of 0.16 m^2. Once the corer was on deck, subsamples of 0.08 m^2 were taken, which were washed on board through a 500-micrometer mesh sieve with previously filtered seawater. The sieved material was fixed with a mixture of seawater and 8% formalin. In the laboratory, specimens were separated from the sediment using an AVEN Mighty Vue Pro 5D ESD magnifying lamp (2.25X magnification) and fine-tipped tweezers. The specimens were kept in vials with 70% alcohol. Subsequently, the polychaetes, whose preservation status allowed it, were identified at the genus level and individuals number were included in the abundance matrix. Taxonomic identification at the genus level was performed using a Zeiss Stemi 508 stereoscopic microscope (maximum magnification 50X) and a Zeiss Primo Star microscope in addition to specialized literature. The assignment to a trophic guild was after the taxonomic identification and was carried out using specialized literature. The sampling sites geographical location, and depth was registered with ship GPS, and multibeam echosounder, respectively.
Data format	Analyzed
Description of data collection	Two oceanographic cruises based on a systematic sampling design with 63 locations were conducted in the southwestern Gulf of Mexico. The first cruise was carried out on June 3- 27, 2015. Due to logistical reasons, sediment samples were only collected at 60 sites. Biological material of seventeen samples (not included in this data set) was lost before the genus-level identification of the polychaetes was achieved. Polychaetes were not obtained in two locations, besides three samples with organisms no identified at the genus level were not included in the abundance matrix, resulting in 38 sites in the first cruise. The second cruise was carried out on August 31- September 20, 2016. Sediment samples were successful at 60 sites. Polychaetes could not be identified at the genus level in nine locations and were not collected in five sites, so they were not included in the analysis. This resulted in 46 sites with polychaetes identified at the genus level in the second cruise. A common abundance matrix for both cruises was elaborated. In those sites where it was possible to register and identify polychaetes at genus level in both cruises, the organism numbers were summed and standardized to individuals per square meter. In those locations with a single record of any of the cruises, the data was just added to the abundance matrix. In this way a total of 54 sites with polychaetes identified at the genus level were recorded for both cruises. The sites were renamed from one to 54 consecutively. The geographical location and depth were registered with ship GPS and multibeam echosounder EM302, respectively, at the time the corer reached bottom.

(*continued on next page*)

Data source location

- Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México
- Southern Gulf of Mexico
- México

Site	Longitude W	Latitude N
1	93.4971	18.9898
2	94.0183	19.0093
3	94.5077	18.7427
4	94.9991	18.8284
5	95.5017	19.0283
6	94.9799	19.1478
7	93.516	19.5089
8	94.0166	19.5116
9	94.5069	19.5128
10	94.9963	19.4969
11	95.5051	19.4992
12	96.0114	19.5083
13	96.0051	20.0064
14	95.5155	20.0012
15	94.5154	19.9996
16	94.0306	20.0211
17	93.0128	20.0034
18	92.5696	20.5033
19	93.5075	20.4969
20	94.5185	20.4991
21	95.0113	20.4901
22	95.5111	20.4937
23	96.0123	20.5099
24	96.5006	20.403
25	96.5102	20.5161
26	96.0053	21.0042
27	95.0197	20.985
28	94.4945	20.9801
29	93.9818	21.0018
30	93.0018	21.0129
31	92.6268	21.5039
32	93.5061	21.5138
33	94.5227	21.4989
34	95.0251	21.4773
35	96.0152	21.5038
36	96.512	21.5155
37	96.512	22.0091
38	96.0245	22.018
39	95.0248	21.9997
40	94.5235	22.0033
41	94.0463	21.9861
42	93.5309	22.4993
43	94.0283	22.5098
44	94.4936	22.5017
45	94.983	22.4916
46	95.5217	22.4997
47	96.01	22.5054
48	96.5036	22.5009
49	96.0146	23.0109
50	95.5151	22.9864
51	95.0153	22.992
52	94.5171	23.0055
53	94.0106	23.0215
54	93.0106	22.9984

(*continued on next page*)

Data accessibility	Mendeley data Data identification number: https://doi.org/10.17632/bz8dr9cjpt.2 Direct URL to data: https://data.mendeley.com/datasets/bz8dr9cjpt/2
Related research article	***For an article which has been accepted and is in press:*** Quintanar-Retama, O., Armenteros, M., Gracia, A., Diversity and distribution patterns of macrofauna polychaetes (Annelida) in deep waters of the Southwestern Gulf of Mexico, Deep-Sea Research Part I, 181 (2022), doi: https://doi.org/10.1016/j.dsr.2022.103699. [1].

Value of the Data

- These data are new, unique and may serve as a basis for further studies in the Gulf of Mexico. Diversity and ecological studies on a poorly studied area like this is of outmost importance and usefulness for future deep-sea research in the region. Data is of great importance since polychaetes, functional traits, and macrofauna in general, in this deep sea area is scarce and knowledge is necessary for understanding the deep sea ecosystem.
- Researchers, students, and stakeholders interested in the ecology, biodiversity, and resilience of deep-sea benthic communities of the Gulf of Mexico will have the opportunity to use this data as baseline for planning further studies and assessing potential impacts due to human actions. Even more, this data can be useful to enhance knowledge and function of deep-sea communities in other parts of the world
- These data can complement larger data sets on the same taxon (Polychaeta) or on other taxa of the deep sea macrofauna in the Gulf of Mexico or elsewhere. It can be used on studies to relate with other fauna categories like meiofauna or megafauna of the region. It could be useful to make comparisons with scientific research in other areas and integrate a global knowledge of the deep sea.

1. Data Description

Figure 1 shows the contribution percentage of the three general feeding guilds (macrophages in red, microphages in blue, and omnivores in green) recorded in the study area for each of the established depth categories (upper bathyal, middle bathyal, lower bathyal and abyssal). The four bars represent one hundred percent of the abundance recorded in its corresponding depth category and the length of the segment of each color determines the percentage contribution of each trophic guild.

Figure 2 shows the percentage contribution of the eight specific feeding guilds (carnivores/scavengers in red; subsurface deposit feeders in aqua green; suspension feeders in black; surface deposit feeders / subsurface deposit feeders in grey; surface deposit feeders / suspension feeders in pink, surface deposit feeders in green, detritivores in yellow, and omnivores in blue) recorded in the southwestern Gulf of Mexico for each of the established depth categories (upper bathyal, middle bathyal, lower bathyal and abyssal). The four bars represents one hundred percent of the abundance recorded in its corresponding depth category and the length of the segment of each color determines the percentage contribution of each trophic guild.

This graph shows the contribution percentage of the three motility traits (discretely motile in blue, motile in red and sessile in yellow) recorded in the study area in each of the four established depth categories (upper bathyal, middle bathyal, lower bathyal, and abyssal). The four bars represent one hundred percent of the recorded abundance in its corresponding depth category and the length of the segment of each color determines the contribution percentage of each motility trait.

This file presents a taxonomic checklist of the 33 families and 69 genera of polychaetes identified at 54 deep-water sites in the southwestern Gulf of Mexico. This list also contains the name of the taxonomic authority and the year of description for each taxon.

Dataset 1. Polychaeta standardized abundance.

This dataset includes standardized abundance data of 69 polychaetes genera recorded at 54 deep-water sites in the southwestern Gulf of Mexico. Abundance values were standardized to individuals per square meter.

Dataset 2. Sampling sites geographic location and depth data

Geographic and bathymetric data set of the sampling sites. The list includes the name, geographic coordinates and depth recorded at each of the 54 sampling sites.

2. Experimental Design, Materials and Methods

2.1. Sampling and sample processing

The biological material was obtained along two cruises carried out on board the Oceanographic Vessel Justo Sierra of the National Autonomous University of Mexico. The samples were collected using a Reineck-type box corer with an effective area of 0.16 m^2. Once the corer was on deck at each sampling site, a 0.08 m^2 subsample was taken and washed on board through a 500-micrometer mesh sieve with previously filtered seawater. The result of this sieving was fixed with a mixture of seawater and 8% formalin. In the laboratory, the samples were washed with tap water through a 500-micrometer mesh sieve to remove the residue of the used fixative. The extraction of the polychaetes specimens was carried out placing the sediment of each sample in Petri dishes of 15 cm in diameter in small volumes until the sample was finished. To visualize the specimens, an AVEN Mighty Vue Pro 5D ESD magnifying lamp (2.25X magnification) was used. The specimens were separated using fine-tipped tweezers and placed in vials with 70% alcohol.

2.2. Taxonomic checklist

The taxonomic identification was done observing the specimens in Petri dishes of 5 cm in diameter with water under a Zeiss Stemi 508 stereoscopic microscope (maximum magnification 50x). When it was necessary, the specimens (or a dissected portion) were mounted on a slide with a drop of a 70% alcohol-glycerol mixture and a coverslip and were observed with a Zeiss Primo Star optic microscope. Some specimens were temporary stained with Methylene Blue or Shirlastain-A to highlight structures of taxonomic importance. General [2–4] and specialized literature [5–8] was used. The validation of the names of families, genera, and taxonomic authorities, as well as the year of description of each taxon, was carried out using the WoRMS match taxa tool [9].

2.3. Abundance Matrix

In the original study design, 63 sampling sites were considered, however, for logistical reasons, sediment samples were only collected at 60 sites during each of the two oceanographic cruises that constitute this data set. Polychaetes identified at the genus level were collected at 38 sampling sites in SOGOM 1 and 46 in SOGOM 2. The abundance matrix was constructed adding the numbers recorded in both cruises. Thirty common sites in both cruises registered polychaetes identified at genus level. Twenty-four locations only presented polychaetes identified at genus level in one of the two cruises (8 in SOGOM 1 and 16 in SOGOM 2). This made a total of 54 sites with polychaetes identified at genus level. The sites were renamed in a scale order from one to 54 consecutively. The standardization of abundance (individuals per square meter) was done based on the number of each polychaete genus in each site. Genus number of a single cruise location was divided by 0.08, whereas data of the two cruises were added and the result was divided by 0.16.

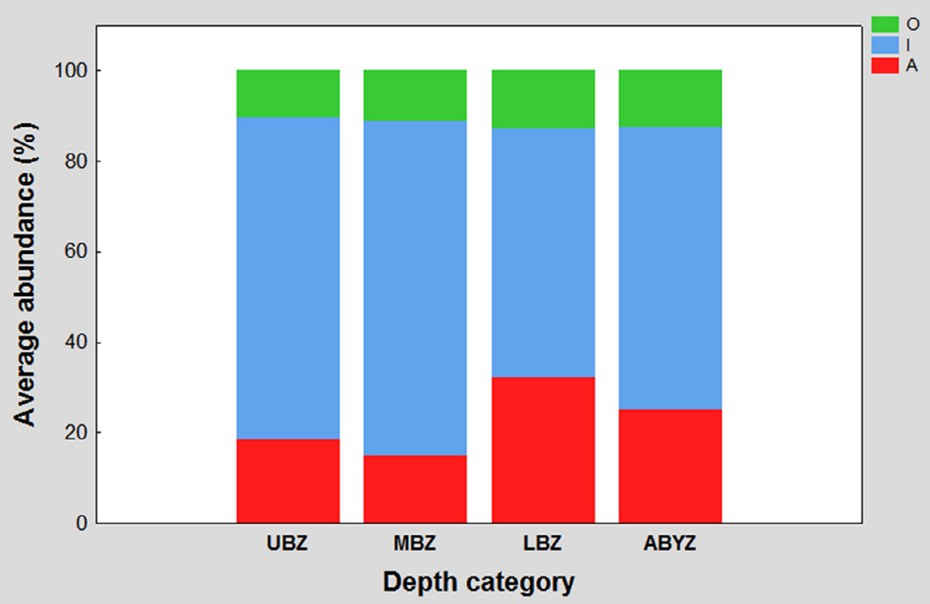

Fig. 1. General feeding guilds contribution percentage to average abundance in each depth category. The letters meaning in the acronym are I = microphages; A = macrophages, and O = omnivores. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); lower bathyal zone (LBZ) and abyssal zone (ABYZ).

2.4. Depth Categories

Four depth categories were determined according to the literature [10,11], and bathymetry of the Gulf of Mexico. These categories were: upper bathyal zone (185 -1000 m); middle bathyal zone (1001 -2000 m); lower bathyal zone (2001 -3000 m), and abyssal zone (3000 – 3760 m). The depth of each sampling site was recorded using the ship multibeam echosounder EM302, and the geographical location with the ship GPS at the time the corer got to the bottom. The depth of the sites with a single fauna record in one of the two cruises was the recorded in the data sampling sites set. An average depth was calculated for sites with data of the two cruises. Each of the 54 sites was assigned to one of the four established depth categories. Thus, 9 sites were classified into the upper bathyal zone, 11 sites in the middle bathyal zone, 16 sites in the lower bathyal zone and 18 sites in the abyssal one, Table 1.

2.5. Stacked bar graphs

The assignment of Polychaeta genera to the feeding guilds was carried out following the proposal of Jumars et al. (2015) [12]. The elaboration of the 100% stacked bar graphs, was done based on the feeding guilds, and motility traits average and subsequently the percentage contribution of each biological trait to the depth categories. Based on this relative abundance matrix, the 100% stacked bar graphs were generated using the STATISTICA 7 software, (Figs. 1, 2, 3).

Table 1
Taxonomic list of genera and families identified in the deep sea from the southwestern Gulf of México.

Phylum Annelida Lamarck, 1802
Class Polychaeta Grube, 1850
Subclass Errantia Audouin & H Milne Edwards, 1832
Order Amphinomida
Family Amphinomidae Lamarck, 1818
Genus *Paramphinome* M. Sars in G. Sars, 1872
Order Eunicida
Family Lumbrineridae Schmarda, 1861
Genus *Abyssoninoe* Orensanz, 1990
Genus *Augeneria* Monro, 1930
Genus *Lumbrinerides* Orensanz, 1973
Genus *Lumbrineris* Blainville, 1828
Family Onuphidae Kinberg, 1865
Genus *Paradiopatra* Ehlers, 1887
Order Phyllodocida Dales, 1962
Family Glyceridae Grube, 1850
Genus *Glycera* Grube, 1850
Family Goniadidae Kinberg, 1866
Genus *Goniada* Audouin & H Milne Edwards, 1833
Genus *Goniadides* Hartmann-Schröder, 1960
Genus *Progoniada* Hartman, 1965
Family Hesionidae Grube, 1850
Genus *Hesiocaeca* Hartman, 1965
Genus *Syllidia* Quatrefages, 1865
Family *Nephtyidae* Grube, 1850
Genus *Aglaophamus* Kinberg, 1866
Genus *Nephtys* Cuvier, 1817
Family Nereididae Blainville, 1818
Genus *Ceratocephale* Malmgren, 1867
Family Paralacydoniidae Pettibone, 1963
Genus *Paralacydonia* Fauvel, 1913
Family Phyllodocidae Örsted, 1843
Genus *Eteone* Savigny, 1822
Family Pilargidae Saint-Joseph, 1899
Genus *Ancistrosyllis* McIntosh, 1878
Genus *Litocorsa* Pearson, 1970
Genus *Sigambra* Müller, 1858
Family Sigalionidae Kinberg, 1856
Genus *Pholoides* Pruvot, 1895
Family Syllidae Grube, 1850
Genus *Exogone* Örsted, 1845
Genus *Pionosyllis* Malmgren, 1867
Subclass Sedentaria Lamarck, 1850
Infraclass Canalipalpata Rouse & Fauchald, 1997
Order Sabellida Levinsen, 1883
Family Sabellidae Latreille, 1825
Genus *Euchone* Malmgren, 1866
Order Spionida Rouse & Fauchald, 1997
Family Spionidae Grube, 1850
Genus *Aonides* Claparède, 1864
Genus *Dispio* Hartman, 1951
Genus *Laonice* Malmgren, 1867
Genus *Malacoceros* Quatrefages, 1843
Genus *Paraprionospio* Caullery, 1914
Genus *Prionospio* Malmgren, 1867
Genus *Spiophanes* Grube, 1860
Family Longosomatidae Hartman, 1944
Genus *Heterospio* Ehlers, 1874
Family Poecilochaetidae Hannerz, 1956
Genus *Poecilochaetus* Claparède in Ehlers, 1875
Family Trochochaetidae Pettibone, 1963

(*continued on next page*)

Table 1 (*continued*)

Genus *Trochochaeta* Levinsen, 1884
Order Terebellida Rouse & Fauchald, 1997
Family Ampharetidae Malmgren, 1866
Genus *Ampharete* Malmgren, 1866
Genus *Amphicteis* Grube, 1850
Genus *Auchenoplax* Ehlers, 1887
Genus *Eclysippe* Eliason, 1955
Family Cirratulidae Ryckholt, 1851
Genus *Aphelochaeta* Blake, 1991
Genus *Chaetozone* Malmgren, 1867
Genus *Kirkegaardia* Blake, 2016
Family Fauveliopsidae Hartman, 1971
Genus *Laubieriopsis* Petersen, 2000
Family Flabelligeridae de Saint-Joseph, 1894
Genus *Bradabyssa* Hartman, 1967
Genus *Diplocirrus* Haase, 1915
Family Sternaspidae Carus, 1863
Genus *Caulleryaspis* Sendall & Salazar-Vallejo, 2013
Genus *Sternaspis* Otto, 1820
Family Trichobranchidae Malmgren, 1866
Genus *Terebellides* Sars, 1835
Infraclass Scolecida Rouse & Fauchald, 2001
Family Capitellidae Grube, 1862
Genus *Mediomastus* Hartman, 1944
Genus *Neoheteromastus* Hartman, 1960
Genus *Neomediomastus* Hartman, 1969
Genus *Notomastus* M. Sars, 1851
Genus *Paraleiocapitella* M. Sars, 1851
Family Cossuridae Day, 1963
Genus *Cossura* Webster & Benedict, 1887
Family Magelonidae Cunningham & Ramage, 1888
Genus *Magelona* F. Müller, 1858
Family Maldanidae Malmgren, 1867
Genus *Sabaco* Kinberg, 1866
Family Opheliidae Malmgren, 1867
Genus *Ammotrypanella* McIntosh, 1878
Genus *Ophelia* Savigny, 1822
Genus *Ophelina* Örsted, 1843
Genus *Tachytrypane* McIntosh <i>in</i> Jeffreys, 1876
Family Orbiniidae Hartman, 1942
Genus *Califia* Hartman, 1957
Genus *Scoloplos* Blainville, 1828
Family Paraonidae Cerruti, 1909
Genus *Aricidea* Webster, 1879
Genus *Cirrophorus* Ehlers, 1908
Genus *Levinsenia* Mesnil, 1987
Genus *Paradoneis* Hartman, 1965
Genus *Paraonides* Cerruti, 1909
Family Scalibregmatidae Malmgren, 1867
Genus *Asclerocheilus* Ashworth, 1901
Genus *Pseudoscalibregma* Ashworth, 1901
Family Travisiidae Hartmann-Schröder, 1971
Genus *Travisia* Johnston, 1840

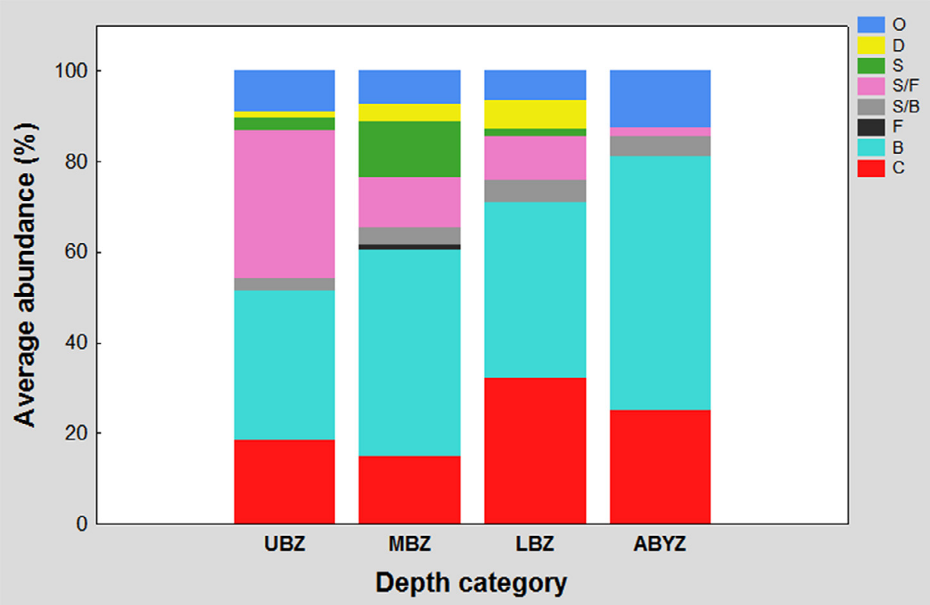

Fig. 2. Specific feeding guilds contribution percentage to average abundance in each depth category. The letters meaning in the acronym are B = subsurface deposit feeders; S = surface deposit feeders; F = suspension feeders; O = omnivores, D = detritivores, and C = carnivores/scavengers. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); lower bathyal zone (LBZ) and abyssal zone (ABYZ).

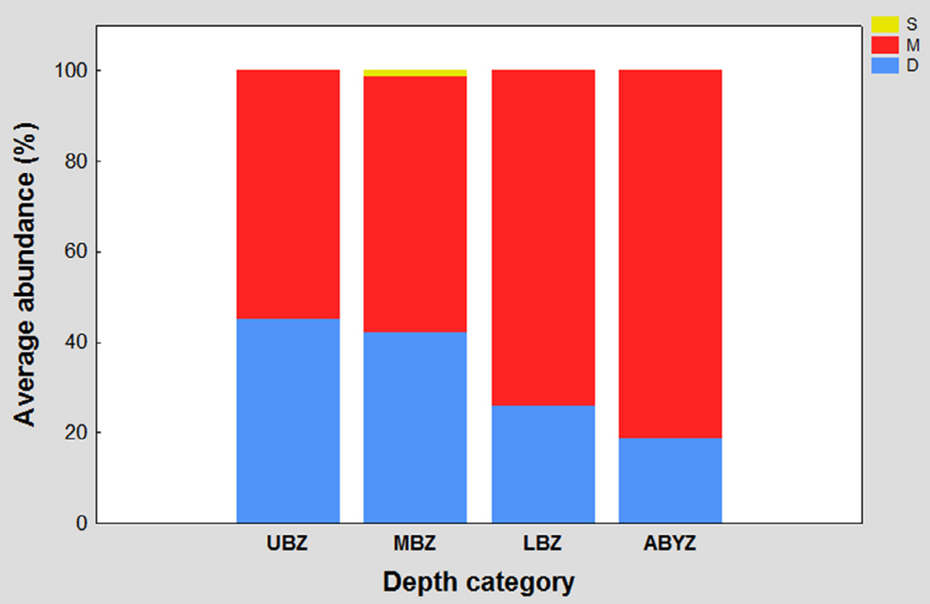

Fig. 3. Motility traits percentage contribution to average abundance in each depth category. The letters meaning in the acronym are M = motile; D = discretely motile, and S = sessile. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); lower bathyal zone (LBZ) and abyssal zone (ABYZ).

Ethics Statements

The authors declare that the manuscript adheres to Ethics publishing standards.

CRediT Author Statement

Octavio Quintanar-Retama: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, and visualization. **Ana Rosa Vázquez-Bader**: conceptualization, methodology, and writing – Review & editing. **Adolfo Gracia**: Conceptualization, Methodology, Investigation, Resources, Writing – Review & editing, Supervision, Project Administration, and Founding acquisition.

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

Polychaete dataset of the southwestern Gulf of Mexico including: taxonomic checklist, abundance, bathymetric distribution, functional diversity, geographic location, and sampling sites depth (Original data) (Mendeley Data).

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Macrofauna abundance and diversity patterns of deep sea southwestern Gulf of Mexico

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The diversity and distribution of macrofaunal communities in the deep-sea bottoms of Gulf of Mexico (GoM) Mexican waters are poorly known compared to the northern GoM. This study was designed to contribute to the knowledge of macrofauna communities through (i) evaluate the taxonomic composition of macrofauna communities at major taxa level, and (ii) analyze the spatial distribution patterns in the deep sea of the southwestern GoM. Benthic macrofauna composition was analyzed in a large geographical area (92.67°–96.70° W 18.74°–23.04° N) and bathymetric gradient (185-3740 m depth). Samples were collected on board the R/V Justo Sierra (Universidad Nacional Autónoma de México) with a Reineck-type box corer during the oceanographic cruises SOGOM-3 and SOGOM-4 carried out on April 21–May 15, 2017, and on August 29–September 20, 2018, respectively. Thirteen environmental parameters were measured (among them, depth, salinity, temperature, O2, sediment grain size, hydrocarbons, and organic matter). Twenty-five taxa were registered in SOGOM 3 (2315 individuals) all of which were observed in SOGOM 4 (1721 individuals) with exception of the mollusk Class Solenogastres. The average abundance (ind. m^{-2}) registered was 517 (range: 150-1388 ind. m^{-2}), and 347 (range: 38-1088 ind. m^{-2}) for SOGOM 3, and SOGOM 4, respectively. In SOGOM 3 Polychaeta, Nematoda, Amphipoda, Tanaidacea, and Bivalvia contributed with 75% of the total abundance, which were also the most abundant in SOGOM 4 representing 82% of total macrofauna abundance. Highest abundance was registered to the south of the study area near the coast, and the lowest one was found in deeper areas. Macrofauna abundance decreased with depth in both cruises. High diversity values were registered at intermediate depths in the south and west zones of the study area. Both cruises separated in a nMDS analysis. During SOGOM 3 dissolved oxygen, aromatic hydrocarbons, and organic matter (%) were the environmental variables related to macrofauna whereas, in SOGOM 4, depth was the most important one. This study fills a gap in the knowledge of diversity and distribution of macrofaunal communities of the deep-sea bottoms of a large area covering the whole bathymetric range of southern Gulf of Mexico and provides a baseline useful to compare with polluted areas and for assessing the impact of chronic pollution and/or potential oil spill accidents.

KEYWORDS

deep sea, macrofauna, diversity, abundance pattern, Gulf of Mexico

1 Introduction

The deep sea greater than 200 m depth (Gage and Tyler, 1991; Fiege et al., 2010) represents 90% of the planet oceans. This ecosystem has unique characteristics like high hydrostatic pressure, low temperature conditions, and scarce and intermittent food availability (Gage and Tyler, 1991; Ramirez-Llodra et al., 2010; Danovaro et al., 2014). The substrate of this ecosystem is mostly composed of soft sediments (Gray, 2002). Consequently, the soft deep sea bottoms benthic macrofauna communities constitute one of the largest faunal assemblages on the planet in terms of area covered (Snelgrove, 1998). These communities are integrated of metazoans with a length of less than 1.5 cm which are retained on a mesh size sieve between 250 and 500 µm (Hessler and Jumars, 1974; Rex, 1981; Gage, 2001; Rex et al., 2006). Typically, a dozen phyla are the most frequent (Grasle, 1991). Polychaetes, peracarid crustaceans, and mollusks stand out for their importance in terms of abundance and diversity (Grassle and Maciolek, 1992; Brandt et al., 2018). They participate in the secondary production, bioturbation, and bio-irrigation sediment processes (Snelgrove, 1998; Zhang et al., 2010), contributing to the transport, burial, and pollutant absorption (Snelgrove, 1998; Banta and Andersen, 2003). Once the pollutants are ingested by organisms, they can be bioaccumulated and hence could affect entire food chains (Somero, 1992). Also, they take part in the organic matter (OM) sink process and oxygen transport to subsurface layers (Crawshaw et al., 2019) promoting bacterial activity (Parkes et al., 1994). Moreover, they affect sediment transport through the increase of system's susceptibility to erosion (Grant et al., 1982), and can also modify fine sediment by feeding and transforming it into larger defecated pellets, thereby increasing the porosity of soft bottoms. Thus, the contribution of this communities in biogeochemical cycles through nutrients recycling, ecological interactions, and environment transformation is fundamental for sustaining the deep sea, and the global oceanic ecosystem.

According to Qu et al. (2016), the distribution of benthic communities in the deep sea of the Gulf of Mexico (GoM) are quite well known and it is possible to predict the abundance, species composition, and biodiversity depending on the locality, and depth. Several studies have been carried out in the northern gulf (Rowe et al., 1974; Pequegnat et al., 1990; Baguley et al., 2006a; Baguley et al., 2006b; Baguley et al., 2008; Wei et al., 2010a; Wei et al., 2010b; Sharma et al., 2011; Wei et al., 2012b; Wei et al., 2012a; Carvalho et al., 2013). The macrofauna abundance tends to decrease with increasing depth. This has been reported in other seas (Baldrighi et al., 2014), in the northern Gulf of Mexico (Wei et al., 2012a) and within the study area (Escobar-Briones et al., 1999). On the other hand, diversity frequently exhibits a bathymetric pattern with lowest values in the upper bathyal and abyssal regions and highest ones at intermediate depths (Rex, 1981; Ramirez-Llodra et al., 2010; Wei and Rowe, 2019). Despite of these general patterns, other trends have been reported, frequently in studies based on the analysis of transects (Pérez-Mendoza et al., 2003). These changes usually were associated with horizontal variations of some abiotic factors such as sedimentation rate or organic matter content. However, there are only a few studies on deep-sea macrofauna communities in the Exclusive Economic Zone of Mexico (but see, Escobar-Briones et al., 2008; Escobar-Briones et al., 1999; Salcedo et al., 2017, Hernández-Ávila et al., 2021). So, the diversity and distribution of macrofaunal communities in the deep-sea bottoms of GoM Mexican waters are poorly known compared to the northern GoM. Recently there is a renewed interest to study the GoM and have a comprehensive knowledge of the whole Large Ecosystem and its responses to different stressors. Among them, oil spills like the two mega oil spills occurred in the GoM (Ixtoc 1, 1979-1980 and DHW, 2010). Events of this magnitude could be repeated and are of great concern due to the impacts on deep-water 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 macrofauna communities through (i) evaluate the taxonomic composition of macrofauna communities at major taxa level, and (ii) analyze the spatial distribution patterns in the deep sea of the southwestern GoM. Data obtained of the large bathymetric and geographic range covered in the southern GoM will contribute substantially to the knowledge of macrofaunal communities in this poor studied area supplying unique information for understanding the GoM as a whole ecosystem. Besides it will provide a baseline data that could be useful to evaluate the impact of man driven activities such as accidental oil spills and/or long-term ecosystem changes.

2 Materials and methods

2.1 Study area

The Gulf of Mexico is one of the most productive and diverse Large Marine Ecosystems of the world (Kumpf et al., 1999) bordered by three nations (US, Cuba, and Mexico). It has an area of about 1,540,000 km2 (Ward and Tunnell, 2017) and a maximum depth near to 4000 m in the central area and the Sigsbee Canyon (Darnell, 2015). Most of the GoM (65%) are deep waters of which 42% corresponds to continental slope (200-3000 m) and 24% to abyssal plains (> 3000m) (Ward and Tunnell, 2017). More than a half of its surface area (55%) is Mexican Economic Exclusive Zone. Deep Gulf bottoms are mainly composed by mud from terrigenous and biogenic origin. The Loop Current coming from the Caribbean Sea determines the Gulf circulation pattern. This current enters through the Yucatán Channel, leaves trough the Florida Straits and produces several cyclonic-anticyclonic gyres of different scales depending on the wind and pressure effects

(Monreal-Gómez and Salas-de-León, 1997). A general net current flows in a West-North-East direction around the Gulf from Campeche Bank to Florida (Monreal-Gómez et al., 2004). Although there is a large number of field and numerical studies carried out over decades in the Gulf of Mexico, the behavior of the Loop Current and the conditions that generate the detachment of the eddies traveling towards the east of the Gulf still lack studies to be predicted with accurate precision. Three important gaps have been pointed out: 1) the non-existence of measurements of the physical oceanographic characteristics (e.g. currents and temperature) in the entire area, in the long term and in the entire water column including atmospheric data of the air-sea interface, 2) the lack of comprehensive measurements of inflows, outflows, counterflow, and underflow and 3) the interaction of the loop current system with west shallow water when it enters to the east and begins to exit the Gulf (NAS, 2018). Freshwater is discharged by several rivers around the Gulf among which the Mississippi River in the North and the Grijalva-Usumacinta River System in the South contribute with the highest load.

2.2 Sampling and sample processing

Sediment samples were collected on board of the R/V Justo Sierra of the Universidad Nacional Autónoma de México (UNAM) in the southwestern GoM during the oceanographic cruises SOGOM-3 and SOGOM-4 carried out on April 21–May 15, 2017 and on August 29–September 20, 2018, respectively. The sampling sites were located within a geographical range of 92.67°–96.70° west longitude and 18.74°–23.04° north latitude, in a depth range from 185 to 3740 m (Figure 1). Sampling design considered 63 locations in each cruise; however, due to logistical reasons only 56 and 62 were successfully sampled in SOGOM 3 and SOGOM 4, respectively. Due to the large area sampled, bathymetric range covered, cast sampling time and ship time cost we limited operating the sampling to one core per site. Original site numbering was kept for cruise comparisons.

The sediment was collected with a Reineck-type box corer of 0.16 m^2 effective area. A sediment sample of 0.08 m^2 surface and 13 cm depth was collected for faunal analysis in each core. Approximately 1000 cm^3 of sediment were collected for abiotic parameters measurement. Faunal samples were sieved on board with filtered seawater through a mesh size of 500 μm and subsequent fixation was made with a mix of seawater and 8% formaldehyde. The 500 μm mesh size retained most of the macrofauna adult organisms and are directly comparable to other studies (e.g. Hernández-Ávila et al., 2021) using this mesh size.

Thirteen environmental variables were measured. Four were registered *in situ*. Depth (m) was determined with the ship's echo sounder. Salinity (PSU), temperature (°C), and dissolved oxygen (ml l^{-1}) of bottom water were measured with a CTD underwater unit (Model Sea-Bird SBE 9 plus). For safety reasons the CTD was placed on average at 282 m (range: 5–780 m) and 159 m (range: 5–552 m) from the bottom, depending on the depth site in SOGOM 3 and SOGOM 4, respectively. At low depths the CTD was closer to the bottom (~5m), so parameters

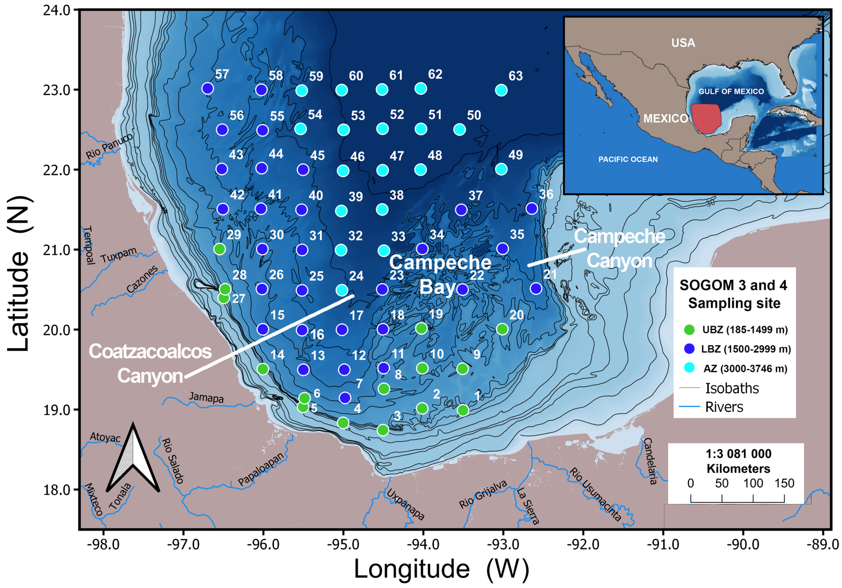


FIGURE 1
Location of the 63 sites sampled during the oceanographic cruises SOGOM 3 and SOGOM 4.

of water were adequately reflected. Registers at deep sites are also reliable of the water mass near the bottom as variations are relatively lower. The geographic location (latitude and longitude) was recorded at the time the corer reached the seabed.

The content of carbonate was estimated by back titration. Excess hydrochloric acid was used to drive off the carbon dioxide produced in the reaction by boiling and the remaining unreacted acid was titrated with a sodium hydroxide solution, in the presence of the phenolphthalein indicator. Organic matter was estimated through the reaction on one dry gram of sediment with 10 ml of potassium dichromate, 10 ml of sulfuric acid, 100 ml of distilled water and 10 ml of phosphoric acid. One ml of diphenylamine was added, and then organic matter and carbon were estimated based on a titration with a 0.5 N ferrous sulfate (Jackson, 1958). Sediment granulometry was measured using a Beckman Coulter model LS 230 laser diffraction analyzer (Small Volume Modulo Plus), and the particle size distribution was expressed as percentage of sand, silt, and clay.

After drying and grinding sediment samples, hydrocarbons were extracted using an ASE 350 accelerated solvent extractor with dichloromethane. The samples were purified and concentrated in a chromatographic column packed with sulfite, silica, alumina, and copper. Concentrated extracts were analyzed with a GC-MS system (Agilent 6809N/5973MS) with Hp-5MS column of 30 m to determine aliphatic, and aromatic hydrocarbon concentration (µg kg^{-1}). Isotopic Carbon was extracted following the standard procedures of combustion. The CO2 was purified with liquid nitrogen −190°C and analyzed with a mass spectrometer to determine the isotopic carbon (13C/12C).

In the laboratory, the sediment was examined using an AVEN Mighty Vue Pro 5D ESD magnifying lamp (2.25X magnification). The specimens were picked up with fine point tweezers and preserved in vials with ethanol 70%. Macrofauna organisms were observed under a stereomicroscope Zeiss Stemi 508 (maximum magnification 50X) and Zeiss Primo Star microscope and identified at the major taxa level using the general taxonomic literature (e. g. Brusca and Brusca, 2003). Only the identified fauna was included in the analysis. Colonial organisms belonging to the phyla Cnidaria, Porifera and Bryozoa were counted as one specimen because we did not know for sure if there could be more than one colony. The taxon names of the organisms were cross-checked with the World Register of Marine Species (WoRMS, www.marinespecies.org).

2.3 Data analysis

The sites of each cruise were organized in three depth categories (DCs): upper bathyal zone (UBZ) (185–1500 m), lower bathyal zone (LBZ) (1501–3000 m), and abyssal zone (AZ) (3001–3740 m). The limit between bathyal and abyssal regions at 3000 m was based on the literature (e.g., Harris, 2020; Watling et al., 2013) and bathymetry of the GoM.

We constructed a grouped line chart for each abiotic factor to assess depth related and between cruises variations. Abundance was standardized to individuals per square meter for each site in both cruises. Based on these, we elaborated a box plot, and pie chart, to evaluate possible macrofauna abundance variations between cruises. Boxplots were notched to show significant differences between DCs or between cruises. The overlap of the notches indicates that the differences are not significant and the non-overlap indicates the opposite (Mcgill et al., 1978; Kampstra, 2008). Besides, we constructed basic, and percent stacked bar plot to analyze registered macrofauna abundance, and relative abundance (percentage contribution of each taxon to the total macrofauna abundance at each site) bathymetric changes within each cruise, and between them with STATISTICA 7 software. The correlation between each abiotic factor, general abundance and polychaete relative abundance values with depth for each cruise was evaluated using Spearman's correlation including the hypothesis test (H0: $r_s = 0$ (there is no relationship); H1: $r_s \neq 0$ (there is a relationship) to assess whether or not the correlation was significant. Values less than 0.4 were defined as weak correlation, between 0.41 and 0.69 intermediate correlation, and values greater than 0.69 as strong correlation. Kruskal-Wallis tests were carried out to determine the significance of the possible abundance and diversity metrics differences observed across cruises and/or depth zones.

For each cruise, the standardized abundance data matrix was square-root transformed to reduce the bias of outliers. Subsequently, we generated a matrix of pairwise similarity between sites based on the Bray-Curtis index (Clarke et al., 2014), and posteriorly a non-metric multidimensional scaling (nMDS). A hierarchical cluster analysis (group average) was performed based on the similarity matrix including the SIMPROF test (1000 permutations for average profile, 999 simulation permutations and 5% level of significance). The cluster analysis was plotted on the nMDS ordination. The nMDS of both oceanographic cruise sites was done from a matrix including both samplings, each one labeled with the respective cruise number (3 or 4) and DCs. Also, an ANOSIM analysis was carried out to test differences among cruises and DCs. Draftsman plot and correlation matrix for environmental parameters were calculated to analyze covariance between them. Values of the correlation coefficient greater than 0.7 were considered strong correlations. The Spearman rank correlations (SR) between matrices of biotic and abiotic similarities were calculated using the BEST routine (Clarke et al., 2008). The abiotic similarity matrix was generated with Euclidean distance from the normalized matrix of environmental variables. Multivariate analyses were carried out with PRIMER v6 (Clarke and Gorley, 2006). Abundance rank curves of each cruise were based on the standardized abundance matrix ordering taxa in each depth category (DC) according to their contribution to the recorded abundance.

Based on the abundance data matrix we calculated diversity estimates (Hill numbers) of order q = 0, 1, and 2 with the iNEXT

TABLE 1 Number of sites, specimens, and taxa. Average abundance and depth for each cruise.

Cruise	Number of sites	Number of specimens	Number of taxa	Average abundance (ind. m^{-2})	Average depth (m)
SOGOM 3	56	2186	25	488 (range: 113-1388)	2155 (range: 185-3740)
SOGOM 4	62	1689	24	341 (range: 38-1088)	2292 (range: 189-3740)

package (Chao et al., 2014) in R. Hill numbers include the three most widely used diversity metrics: species richness (q = 0), Shannon diversity (q = 1) and Simpson diversity (q = 2). Diversity variations among DCs in each cruise were evaluated with rarefaction and extrapolation sampling curves for three Hill numbers. The criterion used for determining the significance between the estimated values of taxonomic richness (0.995 sample coverage) among DCs within each cruise and between cruises was the overlapping confidence interval (no overlapping = significant difference and partial/total overlapping = no significant differences) (Zar, 2010).The geographic distribution abundance map was elaborated with the standardized abundance, whereas the diversity geographic distribution map was done with the estimated taxonomic richness values (q = 0) at 0.8 sample coverage. The resolution of the isobaths for all maps were: 10 m in the 0 to 50 m depth range, 50 m in the 50 to 100 m, 100 m in the 100 to 500 m and 500 m in the 500 to 3500 m intervals. The geographic distribution maps of sample sites, abundance and taxonomic richness were made with the QGIS 3.12 software (QGIS.org, 2021). In the case of the abundance and taxonomic richness maps, the data class aggrupation was carried out with the natural rupture methodology (Jenks) (Smith et al., 2015). All images were edited with Adobe Photoshop CS6 (13.0) software.

3 Results

3.1 Abiotic factors

The abiotic factors measured in the bottom water showed no variation in depths greater than 1000 m. We registered a temperature range between 17.8-5.17°C at 185-1143 m, and 18.69-5.14°C at 189-1225 m in SOGOM 3, and SOGOM 4, respectively. Beyond these depths, temperature always was near to 4°C in both cruises. Temperature and depth correlation was negative and strong in SOGOM 3 and was not significant in SOGOM 4 (r_{s3} = -0.71, $p < 0.001$ and r_{s4} = -0.17, p = 0.19) (r_{s3} = Spearman's correlation coefficient during SOGOM 3; r_{s4} = Spearman's correlation coefficient during SOGOM 4). Salinity values were in a 36.54-35.24 PSU range between 185 to 672 m depth, and 36.45-35.1 PSU from 189 to 614 m in SOGOM 3, and SOGOM 4, respectively. Salinity values were always near to 35 PSU in higher depths for both cruises. Salinity and depth correlation was not significant in both cruises (r_{s3} = -0.19, p = 0.16 and r_{s4} = -0.02, p = 0.90). Dissolved oxygen concentrations registered in SOGOM 3 were found in a 2.48-3.56 ml l^{-1} range at depths of 185 to 1275 m. In deeper locations, dissolved oxygen values showed a 4.0-4.7 ml l^{-1} range, except in the sites 8, and 10 where they registered 3.6 and 5.4 ml l^{-1}, respectively. The dissolved oxygen concentration in SOGOM 4 showed values between a 2.5 and 3.8 ml l^{-1} range in a 285-1225 m depth range. Beyond these depths, dissolved oxygen values varied in a 4.3 to 4.7 ml l^{-1} range. Correlation of DO with depth was positive and intermediate in both samplings (r_{s3} = 0.58, $p < 0.001$ and r_{s4} = 0.45, $p < 0.001$) (Figure 2).

Sand content was excluded from the sediment analysis because it was extremely low in both cruises (≤ 0.09% and 0.27% in SOGOM 3 and SOGOM 4, respectively). Content (%) organic matter and silt showed a decreasing pattern related to depth, whereas carbonate and clay values (%) presented an opposite trend, increasing with depth. The OM values presented a range of 1.15% to 2.89% in SOGOM 3, and 1.12% to 3.27% in SOGOM 4. OM and depth correlation was negative

TABLE 2 Number of sites, specimens, and taxa. Average abundance, and depth for each depth category of each cruise.

SOGOM 3

Depth category	Number of sites	Number of specimens	Number of taxa	Average abundance (ind. m^{-2})	Average depth (m)
UBZ	17	866	22	637 (range: 388 -1112)	824 (range: 185 -1482)
LBZ	24	924	25	462 (range: 125 - 1388)	2324 (range: 1629 - 2885)
AZ	15	396	14	354 (range: 150- 663)	3394 (range: 3001- 3740)
SOGOM 4					
Depth category	Number of sites	Total specimens	Number of taxa	Average abundance (ind. m^{-2})	Average depth (m)
UBZ	16	763	21	596 (range: 125-1088)	805 (range: 189-1467)
LBZ	28	692	21	309 (range: 138-800)	2449 (range: 2080-2875)
AZ	18	234	15	163 (range: 38-413)	3451 (range: 3027-3762)

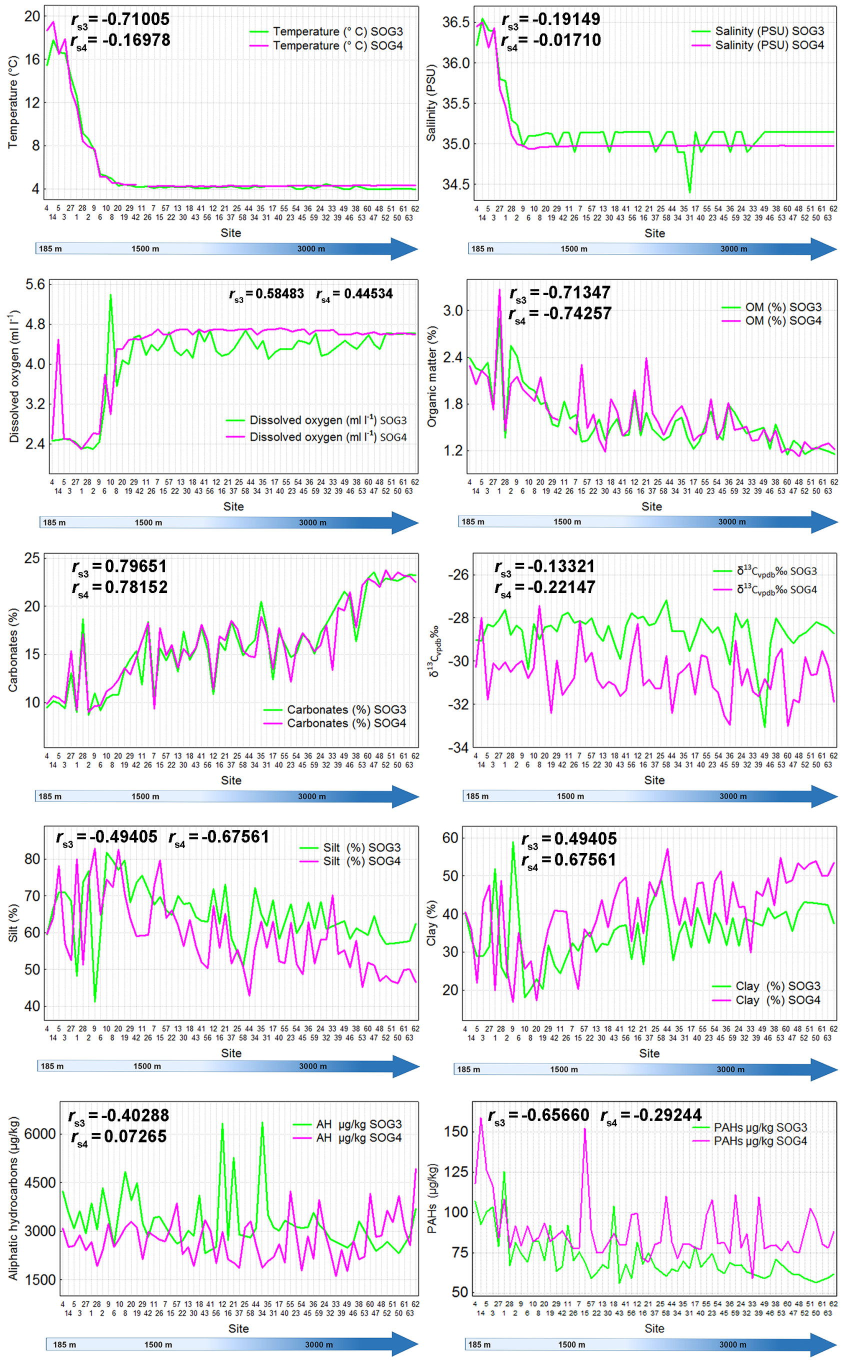


FIGURE 2
Depth related pattern of environmental factors (sites are ordered from low to highest depth, left to right). SOG3 = SOGOM 3, SOG4 = SOGOM 4, AH = Aliphatic hydrocarbons, PAHs = Polycyclic Aromatic Hydrocarbons, r_{s3} = Spearman's correlation coefficient during SOGOM 3, r_{s4} = Spearman's correlation coefficient during SOGOM 4.

and strong in both samplings ($r_{s3} = 0.71$, $p < 0.001$ and $r_{s4} = 0.74$, $p < 0.001$). Silt value range in SOGOM 3 was 41.11%-81.82%, and clay was 18.12%-56.89%. Meanwhile, in SOGOM 4 the silt range was 42.90%-82.86% and clay 16.87% - 57.10%. Silt and depth correlation was negative and intermediate (r_{s3} = -0.49, $p < 0.001$ and r_{s4} = -0.68, $p < 0.001$) while, clay and depth correlation was positive and intermediate in both cruises ($r_{s3} = 0.49$, $p < 0.001$ and $r_{s4} = 0.68$, $p < 0.001$) Content (%) carbonate showed an interval from 8.7 to 23.5 in SOGOM 3, and 9.0 to 23.8 in SOGOM 4. Carbonate and depth correlation was positive and strong in both cruises (r_{s3} = 0.80, $p < 0.001$ and r_{s4} = 0.78, $p < 0.001$). In general, the aromatic and aliphatic hydrocarbons recorded values that decreased with depth increase, except in SOGOM 4 where a slight increase of aliphatic hydrocarbons was registered in sites deeper than 3000 m. Aromatic hydrocarbons ranges were 56-125 µg kg^{-1} and 59-158 µg kg^{-1} for SOGOM 3 and SOGOM 4, respectively. Correlation of aromatic hydrocarbons and depth was negative and intermediate in SOGOM 3 and weak in SOGOM 4 (r_{s3} = -0.66, $p < 0.001$ and r_{s4} = -0.29, p = 0.02). Aliphatic hydrocarbons were found in a 2316- 6364 µg kg^{-1} and 1601 to 4927 µg kg^{-1} ranges for SOGOM 3, and SOGOM 4, respectively. Aliphatic and depth correlation was negative and intermediate in SOGOM 3 and no significance was found in SOGOM 4 (r_{s3} = -0.40, $p < 0.001$and r_{s4} = 0.07, p = 0.57). We registered delta C 13 (d13C) values between -33 to -27 CVPDB‰, and -33 to -27 C_{VPDB}‰ in SOGOM 3 and SOGOM 4, respectively. In SOGOM 3 delta C 13 showed a slight decrease related to depth increase, whereas this trend was not observed in SOGOM 4. Delta C 13 and depth correlation was not significant in both samplings (r_{s3} = -0.13, p = 0.33 and r_{s4} = -0.22, p = 0.08) (Figure 2).

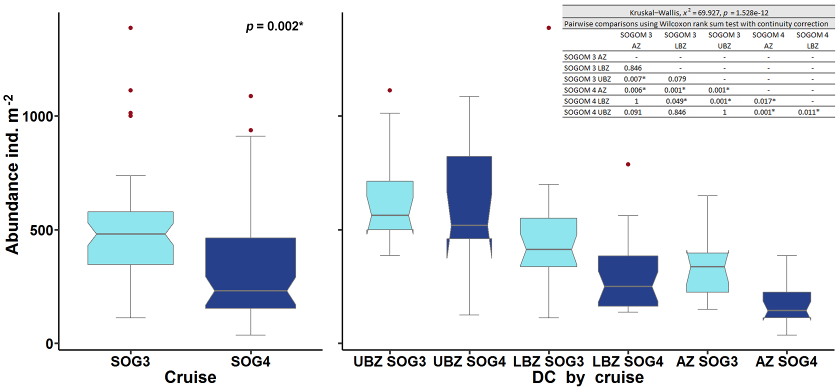
3.2 Fauna description

We registered 25 taxa in SOGOM 3 cruise, all of which were also observed in SOGOM 4 cruise with exception of the mollusk class Solenogastres. During the SOGOM 3 cruise we collected 2186 specimens (range: 9 to 111 per site) in 56 sites, while in the SOGOM 4 cruise we obtained 1689 specimens in 62 sites sampled (range: 3 to 87 per site) (Table 1). Locations grouped by DC showed 866, 924 and 396 individuals, and 22, 25, and 14 taxa for UBZ, LBZ, and AZ, respectively in SOGOM 3, and 763, 692 and 234 individuals, and 21, 21, and 15 taxa for UBZ, LBZ, and AZ in SOGOM 4, respectively (Table 2).

The macrofauna standardized abundance average was higher in SOGOM 3 (488 ind. m^{-2}, range: 113-1388) than in SOGOM 4 (341 ind. m^{-2}, range: 38-1088) and significantly different (p = 0.002) (Figure 3). Abundance difference between cruises was consistent in the three DCs but it was only significant in the deeper ones (Figure 3). Within each sampling, only significant differences were observed between UBZ and AZ in SOGOM 3 while in SOGOM 4 all DCs showed significant differences in recorded abundance (notches in the box plots and p values) (Figure 3). The five most abundant macrofauna taxa were the same in both cruises. Polychaeta, Nematoda, Amphipoda, Tanaidacea, and Bivalvia represented 79% and 84% of the total abundance in SOGOM 3 and SOGOM 4, respectively. The composition of the following five most abundant taxa showed a difference between cruises. Isopoda and Nemertea were found in both cruises, while Bryozoa, Cnidaria and Harpacticoida were recorded in SOGOM 3 and Sipuncula, Porifera and Oligochaeta in SOGOM 4 (Figure 4). Macrofauna abundance presented a decreasing trend related to depth increase in both cruises (r_s = -0.48 and -0.70 ($p \leq 0.001$) in SOGOM3 and SOGOM 4, respectively). Polychaetes, and nematodes were the most abundant taxa in all sites, with exception of sites 26, 58, 59, and 46 in SOGOM 3. Although average abundance was higher in SOGOM3, only two sites (7 and 27) were superior to the highest abundance values registered in SOGOM 4. However, three locations of SOGOM 4 showed lower abundance values that the lower one of SOGOM 3 (Figure 5).

The polychaetes were found in all locations except in site 59 of SOGOM 3. The polychaetes relative abundance decreased with increasing depth in both cruises, but only during SOGOM 3 the correlation between depth and relative abundance was significant (r_s = -0.417, p = 0.001 and r_s = -0.185, p = 0.151 in SOGOM 3 and SOGOM 4 respectively). Nematodes were registered in 96%, and 94% of total sites in SOGOM 3 and SOGOM 4, respectively. This taxon showed a consistent abundance pattern in both cruises with lowest values in the seven shallowest sites, and a relatively higher and uniform abundance in the remaining sites. The Bivalvia mollusk class was registered in 79% of SOGOM 3 sites and in 68% of SOGOM 4 locations. Although absent in some sampling sites, this taxon was recorded in practically the entire bathymetric range with low relative abundance variation. Bivalvia relative abundance mainly varied in a 1%-17% range in both cruises, except sites 46 and 26 of SOGOM 3 and site 62 of SOGOM 4 that showed high relative values of 25%, 35% and 33%, respectively. Tanaidacea (Peracarida, Arthropoda) relative abundance showed a similar pattern in both cruises with slight higher values in SOGOM 4 (1% to 40%) compared to SOGOM 3 (1% to 18%). Amphipoda (Peracarida, Arthropoda) presented differences in the relative abundance between both cruises. In SOGOM 3 this taxon was present in 80% of the sites mainly in a relative abundance range of 1%-25%, except for sites 59, 46, and 58 which presented high values of 33%, 38%, and 44%, respectively. In SOGOM 4 this taxon was collected in 57% of the sites. Only the site 44 registered a high relative abundance of 33%, while the remaining sites showed a low relative abundance range of 1% to 13% (Figure 6).

In general, the geographic abundance pattern was similar in both cruises. The highest abundance values were recorded in the south of the study area and locations near to the coastline and the lowest ones were registered in the northern sites. During SOGOM 3 the highest abundance values were recorded at four sites near the coast in the southern region. Intermediate values were associated with locations near the coastline in the southern and northwestern regions, besides sites located in the saline domes zone in the Campeche Bay and the Campeche and Coatzacoalcos Canyon. Low abundance values were recorded in all regions of the study area, particularly in the northern



Kruskal–Wallis, $x^2 = 69.927$, $p = 1.528e\text{-}12$

Pairwise comparisons using Wilcoxon rank sum test with continuity correction

	SOGOM 3 AZ	SOGOM 3 LBZ	SOGOM 3 UBZ	SOGOM 4 AZ	SOGOM 4 LBZ
SOGOM 3 AZ	-	-	-	-	-
SOGOM 3 LBZ	0.846	-	-	-	-
SOGOM 3 UBZ	0.007*	0.079	-	-	-
SOGOM 4 AZ	0.006*	0.001*	0.001*	-	-
SOGOM 4 LBZ	1	0.049*	0.001*	0.017*	-
SOGOM 4 UBZ	0.091	0.846	1	0.001*	0.011*

FIGURE 3
Box plots of macrofauna abundance (ind. m^{-2}) registered in SOGOM 3 (light blue) and SOGOM 4 (navy blue), and in each depth category. Upper bathyal zone (UBZ), lower bathyal zone (LBZ) and abyssal zone (AZ).

region at the abyssal plain. In SOGOM 4, the highest and intermediate abundance values were again recorded at sites near the coast in the southern region, as well as in most of the localities of the Campeche Bay saline domes zone. Low abundance values were found in the northern zone, except of four sites with intermediate values in the northwestern region (Figures 7, 8).

3.3 Multivariate analysis

The SOGOM 3 nMDS analysis showed an overlapping of sampling sites corresponding to the three DCs. The SIMPROF groups plotted on the nMDS allowed to distinguish four groups. Groups I and II were mainly composed of sites near the coast of the southern region and of the UBZ DC. Remarkably, group I sites were characterized by high abundance values. Group III was dominated by AZ sites and some LBZ locations. Group IV included most of sampling sites of the three DCs (Figure 9A).

The nMDS analysis of SOGOM 4 showed a general clearer pattern ordered in a bathymetric gradient (from the upper bathyal zone to the abyssal region) from left to right of the graph. The SIMPROF test of the cluster analysis allowed us to distinguish three main groups: group I composed by sites of the UBZ region and two sites of the LBZ. Group II was dominated by sites of the LBZ region, one site (59) of the abyssal region and five (6, 10, 19, 20 and 29) of the UBZ. Group III showed two sites (9 and 42) of the UBZ and sites of the LBZ and AZ, each one with 13 sampling sites (Figure 9B). The nMDS analysis of both cruises did not show a clear separation between them, although sampling sites of each cruise were ordered at opposite ends (Figure 10). The ANOSIM showed a slight, but significant difference (R = 0.206 p = 0.001) in the composition and structure of the macrofauna communities between cruises. These variations occur fundamentally in the deepest DCs. When comparing UBZ between cruises, no significant differences were found (R = 0.002 p = 0.393), however they were observed comparing LBZ (R = 0.24 p = 0.001) and AZ (R = 0.43 p = 0.001) between SOGOM 3 and 4. When we compared

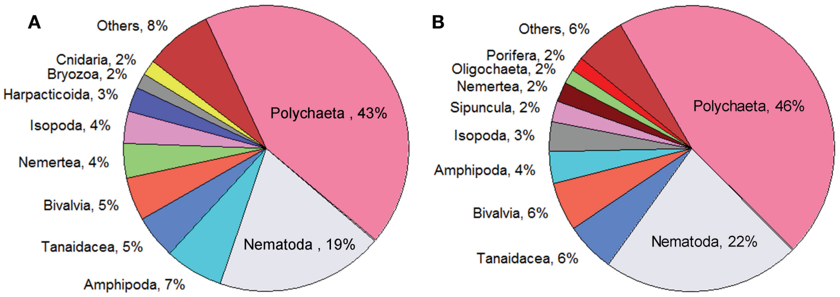


FIGURE 4
Relative abundance of the ten most abundant macrofauna taxa of SOGOM 3 **(A)**, and SOGOM 4 **(B)**.

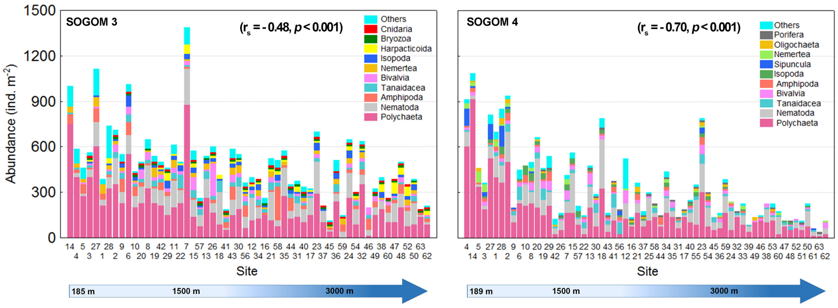


FIGURE 5
Abundance of the ten most abundant macrofauna taxa related to depth in SOGOM 3 and SOGOM 4, r_s = Spearman's correlation coefficient.

within each cruise, the ANOSIM showed the macrofauna communities changes across the bathymetric gradient. The greatest differences were registered when comparing UBZ with AZ (R: 0.231 p = 0.002; R: 0.458 p = 0.001 in SOGOM 3 and 4 respectively), while the smallest ones were recorded between adjoining DCs, particularly between LBZ and AZ (R: 0.046 p = 0.222; R: 0.125 p = 0.012 in SOGOM and 4, respectively).

Abundance rank curves showed bathymetric variations in the composition and structure of the macrofaunal community. In SOGOM 3, the taxa that mainly contributed to abundance were essentially the same (Polychaeta, Nematoda and Amphipoda) in the three DCs. Bivalvia was the fifth taxon in ranking abundance in the three DCs. Sipuncula abundance decreased with increasing depth while Harpacticoida showed the reverse pattern. Porifera and Tanaidacea showed a parabolic shape pattern with the highest contribution to abundance in LBZ and the lowest in UBZ and AZ. In general, during SOGOM 4 Polychaeta, Nematoda and Tanaidacea were the taxa that most contributed to abundance in the three DCs. Amphipoda was ranked fifth in the UBZ and LBZ and sixth in AZ. Bivalvia was sixth in ranking abundance in UBZ and fourth in LBZ and AZ. Sipuncula showed the same pattern as in SOGOM 3 decreasing its contribution to total abundance with increasing depth. Porifera and Harpacticoida again showed an inverse pattern to that of Sipuncula, their contribution to abundance being more important with increasing depth (supplementary data).

The BIOENV analysis included nine abiotic factors (longitude W, depth (m), temperature (°C), dissolved oxygen (ml l^{-1}), polycyclic aromatic hydrocarbons (µg kg^{-1}), aliphatic hydrocarbons (µg kg^{-1}), d13CVPDB‰, organic matter (%) and clay (%)). Four environmental variables were then excluded due to their strong correlation with other abiotic factors. In SOGOM 3, salinity was highly correlated with bottom water dissolved oxygen concentration, and carbonate content with sediment organic matter content. While, in SOGOM 4 the highest correlation was between salinity and temperature, and carbonate with depth. In addition, latitude and sediment silt content were also excluded from the analysis, as they were strong correlated with depth and sediment clay content in both oceanographic cruises, respectively. The environmental parameter combination (up to 4 factors) that showed the best match with biotic similarity matrices using the Spearman rank correlation were temperature, dissolved oxygen, aromatic hydrocarbons, and organic matter in SOGOM 3 with a 0.358 correlation (p = 0.001) with none permuted statistic greater than Rho. Meanwhile, in SOGOM 4 depth was the environmental

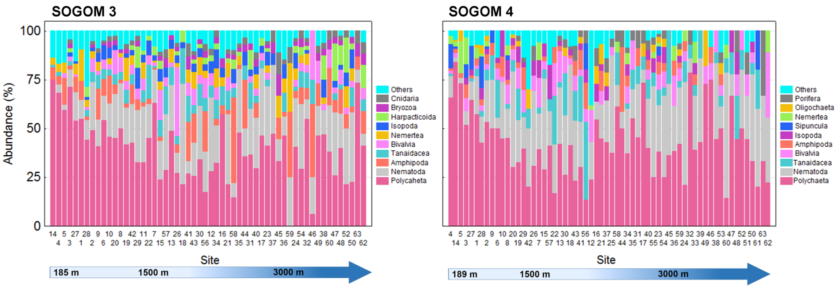


FIGURE 6
Relative abundance of the ten most abundant macrofauna taxa related to depth in SOGOM 3 and SOGOM 4.

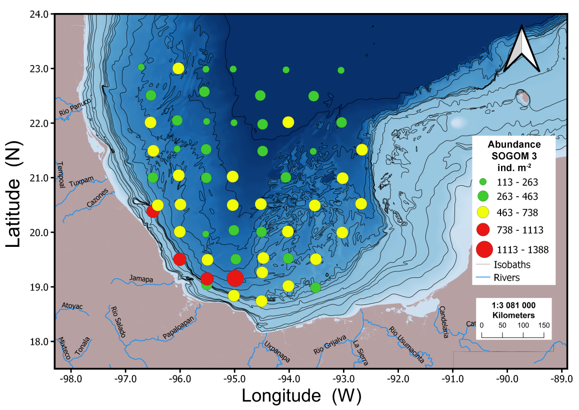


FIGURE 7
Geographic distribution of macrofauna abundance values for SOGOM 3.

parameter that showed better correlation (0.337) with biotic similarity matrices (p = 0.001).

3.4 Biodiversity estimates

In the analysis of diversity we registered a sample coverage higher than 0.996 for all DCs in both cruises, except AZ in SOGOM 4 that registered 0.988 SC. The sampling curves analysis showed that LBZ registered the highest diversity values in both cruises based on the three Hill numbers analyzed (q = 0, 1, 2), also sharing higher values with AZ during SOGOM 3 with q = 2. However, a close comparison (0.995 sample coverage) showed that there were no significant differences of taxonomic richness among DCs during SOGOM 4 and during SOGOM 3 LBZ was more diverse than AZ and did not present significant differences with UBZ. In the case of the Shannon and Simpson diversity, in both cruises, LBZ was more diverse than UBZ and did not present significant differences with AZ. (Figures 11, 12 and Supplementary data).

The diversity profiles of SOGOM 3 based on Hill numbers 0 to 2 showed a range from 20.3 to 4.2 in average Alpha diversity, from 1.2 to 1.0 in Beta diversity, and from 25 to 4.4 in Gamma diversity. The Alpha diversity profile revealed that AZ had more evenness than LBZ, and UBZ (Supplementary data). In SOGOM 4 we registered values between 19.0 and 3.6 in average Alpha diversity, between 1.3 and 1.0 in Beta diversity, and between 24 and 3.7 in Gamma diversity using Hill numbers 0 to 2. The Alpha diversity profile showed that LBZ, and AZ had relative more evenness than UBZ (Supplementary data).

Diversity values (taxonomic richness q = 0) according to geographic distribution in SOGOM 3 showed that low diversity occurred in all regions of the study area. The intermediate values were found in the central region including the Coatzacoalcos Canyon, part of the Campeche Bay saline domes zone, two sites in the Campeche Canyon and five more in the northwestern region. The highest diversity values were associated with localities in the bathyal region in the south and northwest of the study area, besides, one site in the abyssal plain (Figure 13). In SOGOM 4 locations with low diversity records were also spread out along the study area. The highest values were again recorded in the bathyal zone of the northwestern region, two sites in the southwestern region and two more in the abyssal zone. Whereas, in the northern region of the study area, and in the Campeche Bay salt domes zone and in the Campeche Canyon, we registered intermediate diversity values (Figure 14).

4 Discussion

4.1 Abiotic factors

The bottom water environmental variables showed a same pattern in both cruises. Dissolved oxygen, and temperature values registered relative high variation ranges in the 185-1200 m depth interval (range: 2 to 3.5 ml l^{-1}, and 19 to 5° C, respectively) compared to higher depths where variation was minimal (4.0-4.7 ml l^{-1} and temperature close to 4° C, respectively). Also, salinity values stabilized at 35 PSU near 650 m depth in both cruises. These values agree with the North Atlantic Deep Water (NADW) characteristics registered under 1000 m depth with temperature close to 4° C, 35 PSU salinity and dissolved oxygen concentration higher than the overlying layer (Rivas et al., 2005).

Sediment composition varied with depth in both cruises; such pattern consisted in a clay increase, and a silt concentration decrease with increasing depth and with sand values below 0.3%.

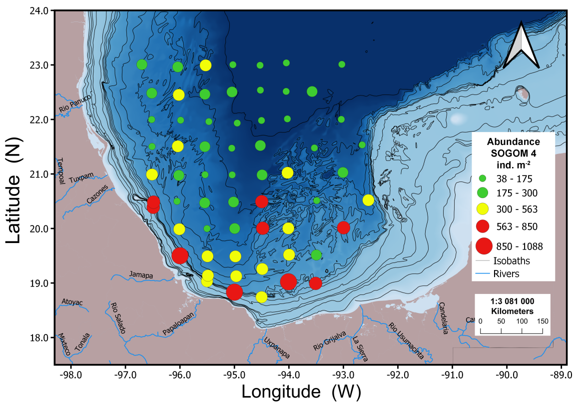


FIGURE 8
Geographic distribution of macrofauna abundance values for SOGOM 4.

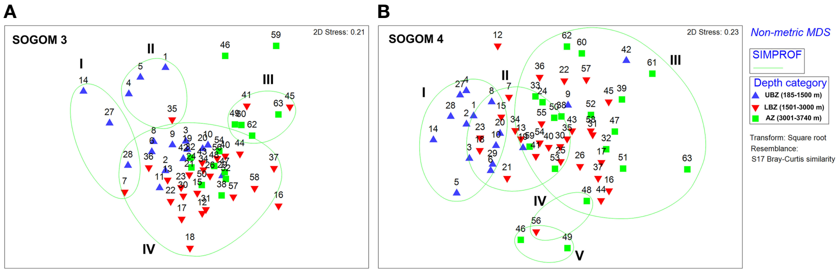
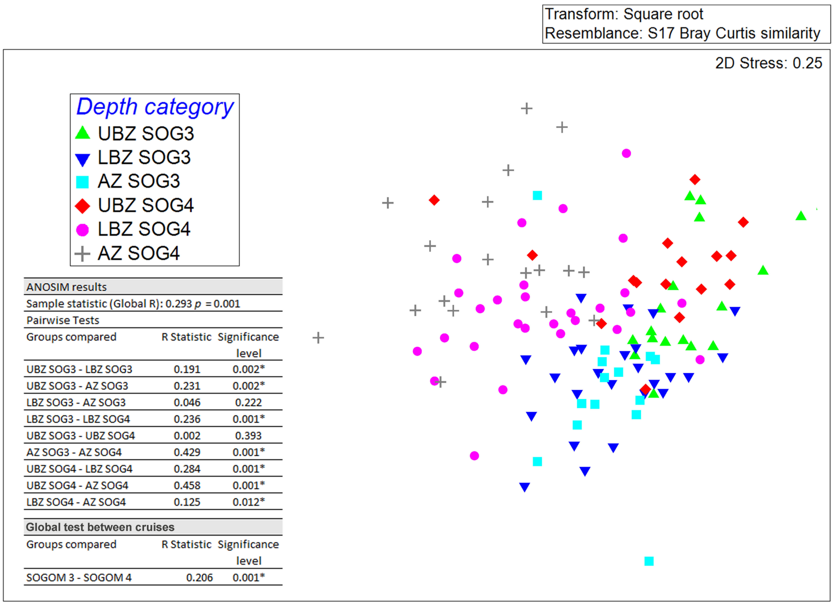


FIGURE 9
Non-metric multidimensional scaling of macrofauna communities of SOGOM 3 **(A)** and SOGOM 4 **(B)** with a classification analysis plotted (green line) based on Bray Curtis similarities. Upper bathyal zone (UBZ-blue triangles), lower bathyal zone (LBZ-red inverted triangles), and abyssal zone (AZ-green square).

This pattern was previously documented in the southwestern GoM (Díaz-Asencio et al., 2019) where terrigenous sediments predominate (Balsam and Beeson, 2003; Díaz-Asencio et al., 2019) with an important component of carbonated biogenic sediments that increase their concentration with depth and distance from the coastline (Balsam and Beeson, 2003). Although we did not record clear variations in sand concentration between cruises, we consistently recorded high silt and low clay concentrations in SOGOM 3 compared to SOGOM 4 in the two deepest DCs. The sediment carbonate concentration also presented a depth-related pattern with the highest values found in the deepest zone of the study area. This pattern agrees to that reported by Balsam and Beeson (2003) who recorded values of up to 50% in the abyssal zone and 75% near the Yucatan shelf.

OM content (%) varied with depth in both cruises; such pattern consisted in highest values in shallower sites close to the coast and lower ones in deeper sites. The $\delta^{13}C$ analysis did not



ANOSIM results		
Sample statistic (Global R): 0.293 p = 0.001		
Pairwise Tests		
Groups compared	R Statistic	Significance level
UBZ SOG3 - LBZ SOG3	0.191	0.002*
UBZ SOG3 - AZ SOG3	0.231	0.002*
LBZ SOG3 - AZ SOG3	0.046	0.222
LBZ SOG3 - LBZ SOG4	0.236	0.001*
UBZ SOG3 - UBZ SOG4	0.002	0.393
AZ SOG3 - AZ SOG4	0.429	0.001*
UBZ SOG4 - LBZ SOG4	0.284	0.001*
UBZ SOG4 - AZ SOG4	0.458	0.001*
LBZ SOG4 - AZ SOG4	0.125	0.012*

Global test between cruises		
Groups compared	R Statistic	Significance level
SOGOM 3 - SOGOM 4	0.206	0.001*

FIGURE 10
Non-metric multidimensional scaling of SOGOM 3 and SOGOM 4 macrofauna communities based on Bray Curtis similarities. Upper bathyal zone (UBZ), lower bathyal zone (LBZ), abyssal zone (AZ). UBZ in SOGOM 3 (green triangle), LBZ in SOGOM 3 (blue inverted triangle), AZ in SOGOM 3 (light blue square), UBZ in SOGOM 4 (red diamond), LBZ in SOGOM 4 (pink circle), AZ in SOGOM 4 (gray cross).

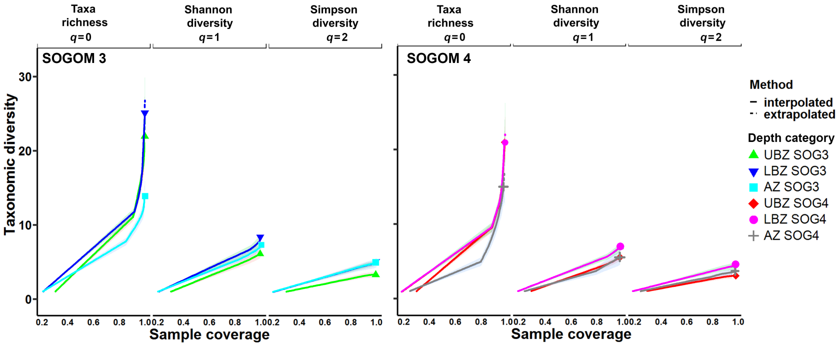


FIGURE 11
SOGOM 3, and SOGOM 4 coverage-based R/E (rarefaction and extrapolation) sampling curves for three Hill numbers (q = 0, 1, and 2). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

give clear results about marine and terrigenous sediment ratios. The values were consistently higher in SOGOM 3. We registered a range of -27.19‰ to -33.06‰ with a -28.63‰ ± 0.8‰ average in SOGOM 3 and a -27.45‰ to -33.01‰ range, and an average -30.63‰ ± 1.1‰ in SOGOM 4. These values could be due to the presence of carbon fixed by chemosynthetic communities (Paull et al., 1985; Brooks et al., 1987; Demopoulos et al., 2010) typical of hydrocarbon infiltration zones which have been recorded in the study area (Sahling et al., 2016). Our results contrast with some records reported by González-Ocampo et al. (2007) (–25.39‰ to –20.95‰, average of –22.9‰ ± 0.9‰) in the region. However, they fit well with data registered by Gracia (2010) in a large area and wide bathymetric range in the southern GoM along ten years whose average varied between-26.62‰ a -31.17‰ in a general range of -24.82‰ a -36.09‰.

Sediment hydrocarbon concentrations varied between cruises. Average aliphatic hydrocarbon value in SOGOM 3 was higher than SOGOM 4 (3347 µg kg^{-1} ± 867 µg kg^{-1} vs. 2739 µg kg^{-1} ± 673 µg kg^{-1}), whereas average aromatic hydrocarbon value was relatively lower in SOGOM 3 compared to SOGOM 4 (72 µg kg^{-1} ± 14 µg kg^{-1} vs. 88 µg kg^{-1} ± 18 µg kg^{-1}). However, a general pattern of higher sediment hydrocarbon concentration in sites located in the southern region near the coast was apparent. This pattern was more consistent in PAHs sediment concentration for both cruises, as high aliphatic hydrocarbons values were recorded in the abyssal zone during SOGOM 4. The high PAH concentrations in the UBZ of the southern area can be explained by the presence of numerous oil seeps found in this area, oil platform activities and the influence of several rivers that introduce pollutants to the marine environment (Gracia et al.,

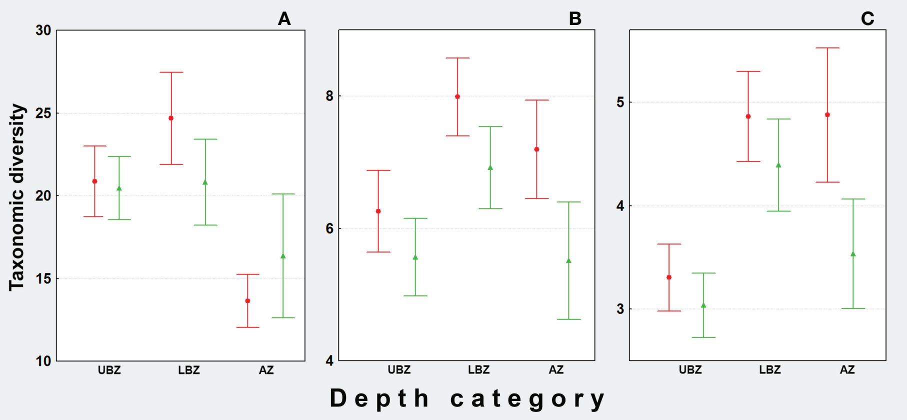


FIGURE 12
Punctual comparison (0.995 sample coverage) of taxonomic richness (*q* = 0) **(A)**, Shannon diversity (*q* = 1) **(B)** and Simpson diversity (*q* = 2) **(C)** during SOGOM 3 (red) and SOGOM 4 (green). Upper bathyal zone (UBZ), lower bathyal zone (LBZ), abyssal zone (AZ).

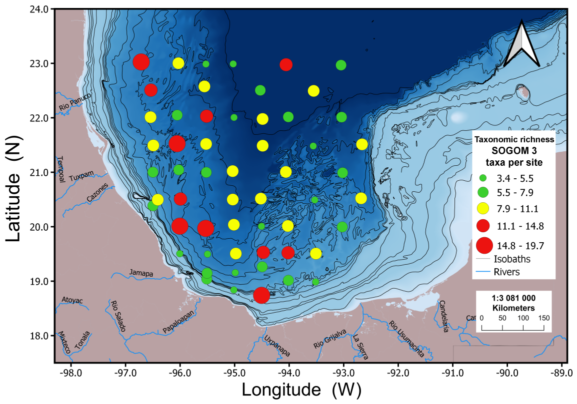


FIGURE 13
Geographic distribution of macrofauna diversity values for SOGOM 3.

2014). The PAH concentration range (56-125 μg kg^{-1}, and 59-158 μg kg^{-1} for SOGOM 3 and SOGOM 4, respectively) is within the range reported for the Southern Gulf of México and, (albeit within the lowest values) within the interval recorded in the adjacent oil platform area (16–953 μg kg^{-1}) located in the continental shelf (Gracia et al., 2016a; Gracia et al., 2016b), and similar to values (84 μg kg^{-1}- 158 μg kg^{-1}) registered in sediments of the deep zone of the north of the GoM (Adhikari et al., 2016). Although PAHs represented a minimal fraction of the total hydrocarbons recorded (3% in SOGOM 3 and 4% in SOGOM 4), they are a fraction of biological importance due to their high toxicity by their mutagenic effects. (Hatami et al., 2021; Billah et al., 2022). In addition, they were among the set of environmental factors most related to the fauna distribution during SOGOM 3. The presence of these pollutants could be influencing the composition of the communities, favoring the presence of taxa capable of resisting their effects to some extent. In the study area, Capitellidae, a taxon documented as tolerant to the presence of some PAHs (Bach et al., 2005), has been recorded as one of the dominant families within the polychaetes (Quintanar-Retama et al., 2022)(also the dominant taxon in this study). In the region, the dominance of deposit feeders has also been documented (Quintanar-Retama et al., 2022), which, due to their bioturbating activity, promote the burial of pollutants, reduce their bioavailability (Timmermann et al., 2008; Konovalov et al., 2010), and favor the establishment of macrofaunal communities.

The UBZ can be characterized as a region that presents important DO concentrations, salinity and temperature variations, high OM and silt concentrations, low carbonate and clay in sediments and high aromatic hydrocarbons values. Whereas the LBZ and AZ regions were described by a high DO, salinity and temperature stability, low OM and silt values, high carbonate and clay values and relatively lower aromatic hydrocarbons in sediments. All these environmental factors have been related to the deep sea benthic communities distribution. Temperature and hydrostatic pressure have been documented as promoters of faunal zonation because they establish a physiological bottleneck that prevents the broad bathymetric distribution of species from shallow areas (Allen, 2008; Brown and Thatje, 2014). Adaptations such as increased mitochondrial concentration and adoption of enzymes more efficiently at low temperatures have been documented (Clarke, 1998). The importance of temperature as a structurer of benthic communities in the deep sea can be seen in the distribution pattern observed in regions such as Antarctica where the bathymetric gradient does not imply a significant temperature gradient and it is very common to record eurybathic species (Brey et al., 1996; Brandt et al., 2007) in such a way that the typical zonation of temperate or tropical regions is not usually recorded. Also, oxygen (Levin and Sibuet, 2012) and the organic matter availability (Cosson et al., 1997; Mamouridis et al., 2011; Bernardino et al., 2016; Brandt et al., 2018; Guggolz et al., 2018) has also been shown to be important factors for the distribution of deep-sea benthic communities.

4.2 Fauna description

The most abundant taxa (Polychaeta, Nematoda, Amphipoda, Tanaidacea and Bivalvia) with polychaete dominance in the macrofauna communities that we registered (43% in SOGOM 3 and 46% in SOGOM4) agrees with those reported in other studies of deep sea macrofauna. (Hessler and Sanders, 1967; Hessler and Jumars, 1974; Alongi, 1992; Brandt and Schnack, 1999; Paterson et al., 2009; Bernardino et al., 2016; Brandt et al., 2018; Brandt et al., 2019, Hernández-Ávila et al., 2021). It is interesting to note that Isopoda was not recorded

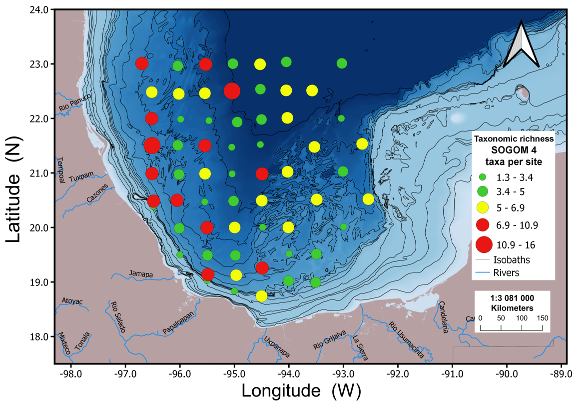


FIGURE 14
Geographic distribution of macrofauna diversity values for SOGOM 4.

within the five most abundant taxa even that it usually is a dominant taxon in the macrofauna (e.g. Brandt et al., 2019). Specially the very diverse and widely deep sea distributed Asellota suborder (Wilson, 2008) which can represent up to 97% of the isopods collected in this environment (Brandt et al., 2007). We recorded a relative isopods abundance lower than tanaidaceans and amphipods (4% in SOGOM 3 and 3% in SOGOM 4). Nonetheless, the isopods were among the six taxa with the highest number of records in both cruises.

The bathymetric pattern of the relative abundance of macrofauna taxa was similar in both cruises. In general, Polychaeta abundance decreased with increasing depth. This trend within the benthic macrofauna communities has already been documented in other seas (Brandt et al., 2018) and in the study area (Quintanar-Retama et al., 2022) and is partly due to the dominance of other groups like crustaceans in the low bathyal, and abyssal regions (Brandt et al., 2018). The polychaetes relative abundance decreasing pattern was more evident up to 2300 m depth. In deeper sites, the polychaete abundance did not show a clear pattern in both cruises, although average values recorded were important (35% in SOGOM 3 and 44% in SOGOM 4). Nematodes showed a same bathymetric pattern in both cruises, characterized by low abundance up to 600 m and by relative high values, in deeper sites. This group is an important component of deep-sea infauna communities (Sharma et al., 2011; Baldrighi et al., 2014) but often it is not considered in macrofauna studies because it is a typical taxon of meiofauna communities (Higgins and Thiel, 1988; Giere, 2008). Even though the genera present in the macrofauna retained in sieves larger than 300 microns are usually different from those retained between 45 and 300 microns, besides, they present lower densities than those reported for typical meiofauna genera (Baldrighi et al., 2014), and carry out important ecological functions within benthic macrofauna communities (Sharma et al., 2011). Tanaidacea is a well-represented taxon in the deep sea (Larsen, 2005) and considered a eurytopic taxon (Blazewicz-Paszkowycz et al., 2012) due to its wide distribution in the marine environment and its presence in freshwater habitats (Bamber, 2008). This taxon presented low relative abundance values up to 800 m, but its contribution to the general abundance increased in deeper sites. Amphipods and harpacticoid copepods, that are well represented in the deep sea (Baguley et al., 2006a; Blankenship et al., 2006) also recorded high values of relative abundance in LBZ and AZ, respectively. According to Brandt et al. (2018), the macrofaunal composition of abyssal regions is frequently dominated by crustaceans. We observed a similar pattern with an increase of the relative abundance of Amphipoda, Tanaidacea and Harpacticoida related to increasing depth, but polychaetes were dominant in the three DCs.

Sponges and sipunculids were among the taxa that showed notable changes in abundance across depth categories. Sponges of the class Hexactinellida are a well-represented and wide distributed taxon in the deep sea (Dohrmann et al., 2008). In this study, Porifera registered a low representation in UBZ, high in LBZ and an intermediate in AZ in both cruises (ratio between records and number of sites were 0.06, 0.67, 0.47 in UBZ, LBZ and AZ during SOGOM 3, and 0.13, 0.71, 0.33 during SOGOM 4, respectively). The sipunculid bathymetric distribution registered a decreasing pattern with high abundance in relative shallow waters, mainly in SOGOM 4, which agrees with the abundance pattern reported in the literature (Baldrighi et al., 2014).

In general, our standardized abundance values were lower compared to available data in other deepwater regions like the South Atlantic (Bernardino et al., 2016), in a wide latitude range of the Atlantic (Sibuet et al., 1989), the Mediterranean Sea (Baldrighi et al., 2014). In the north of the GoM reported abundance values were also higher in the UBZ (Demopoulos et al., 2014), UBZ-AZ (Wei et al., 2012a) and LBZ-UBZ (Washburn et al., 2017) regions compared to our data. In the southern Gulf of Mexico some data reported for the UBZ-AZ area (794-2713 ind. m^{-2}, Escobar-Briones et al., 1999), are within our abundance range but other recorded in the Campeche Canyon (1,550 to 6,925 ind. m^{-2}, Escobar-Briones et al., 2008) and in the northwest region (400-128,000 ind. m^{-2}, Salcedo et al., 2017) are higher. However, these results are not directly comparable because these authors used a mesh sieve of 250 or 300 microns while we used a sieve of 500 microns which could explain the relatively low abundance values we recorded in both cruises. Besides, some of these studies included typical taxa of meiofauna (nematods, copepods and ostracods) or considered all the organisms recovered of the sieved sample such as foraminiferans (Escobar-Briones et al., 2008). A sound comparison should require considering sampling device type, the mesh size used for sieving, the sampling depth and the groups included in the analysis.

The nMDS and ANOSIM analyses showed slight, but significant differences between cruises (R: 0.211) (p = 0.001). Since the communities composition and structure were similar in both cruises, the differences shown by the multivariate analysis could be largely due to the difference in general abundance. The high abundance recorded during SOGOM 3 could reflect a seasonal effect, which is a wide documented phenomenon in the deep sea (Galéron et al., 2009; Billett et al., 2010; Cordes et al., 2010; Glover et al., 2010). The environmental factor analysis revealed high silt and low clay average values in the SOGOM 3 deepest DCs, where the macrofauna abundance variation was more evident between cruises (Figure 5). The granulometric sediment composition was proposed a as driver of macrofauna abundance variations (Baldrighi et al., 2014). Sedimentological composition variations in this study could be related to seasonal changes of continental sediment supply associated to seasonal river discharge.

In both cruises we observed that the macrofauna abundance decreased with increasing depth and decreasing OM. This pattern was widely documented in the deep sea (Hessler and Sanders, 1967; Gage and Tyler, 1991; Wei et al., 2010a; Wei et al., 2012a; Baldrighi et al., 2014; Bernardino et al., 2016) and also related to OM availability with depth (Morse and Beazley, 2008) and distance from the coast (Escobar-Briones and García-Villalobos, 2009) Some authors (Pérez-Mendoza et al., 2003; Hughes and Gage, 2004) have reported inconsistencies to this widespread bathymetric pattern related with local environmental variables that promoted infaunal abundance. We recorded sites that deviated from the abundance general depth-related pattern located in areas with high sedimentation rates (continental rise, Coatzacoalcos Canyon) that promotes the OM accumulation, favouring high abundance (Vetter and Dayton, 1998; Escobar-Briones et al., 2008).

The pattern of abundance geographic distribution was similar in both cruises with the highest values recorded close to the coastline in the southern region, and the lowest ones in the abyssal plain located in the northeastern region of the study area. The Campeche Bay salt domes zone registered intermediate abundance values in SOGOM 3 and intermediate and high in SOGOM 4. In this area the presence of a quasi-permanent cyclonic gyre (Díaz-Flores et al., 2017) promotes nutrient upwellings that enhance primary productivity and a posterior OM exportation to deep sea floor. Also, this area is under the influence of continental OM contribution of the Grijalva Usumacinta river system, the second most important one contributing with water and sediments to the GoM after the Mississippi River. The presence of numerous oil seeps in this area is another factor that may help to understand the abundance pattern. Oil natural flows may allow the establishment of communities based on chemoautotrophic endosymbiotic bacteria, that do not depend on the export of organic matter produced in surface waters or of the continental region (Levin and Michener, 2002; Levin, 2005; Bourque et al., 2017). According to MacDonald et al. (1989) important infaunal abundance values are usually recorded in sites close to this type of environment. In the northwestern region of the study area intermediate abundance values of both cruises could be mainly related to the OM contribution of river discharge on the Veracruz and Tamaulipas coasts (e.g., the Soto la Marina, Pánuco, Tuxpan and Cazones rivers).

4.3 Multivariate analysis

The multivariate analysis showed depth-related differences in the macrofauna community composition and structure in both cruises. These kind of differences were extensively recognized in other deep sea regions (e. g. Levin et al., 2001; Bernardino et al., 2016; Woolley et al., 2016) and in the Gulf of Mexico (e.g. Hernández-Ávila et al., 2021). The separation along the depth gradient was more evident in SOGOM 4. The groups generated by the classification analysis with the SIMPROF test plotted on the ordering obtained for each of the samplings, confirmed this depth pattern. It must be noted that, even though the specimens were identified at a high taxon level, this pattern was detected. According to Brandt et al. (2019) this taxonomic resolution degree may not be useful to show the differences between basins, but it is usually enough to show the differences between different depth zones. Differences were similar between cruises. Polychaeta, Nematoda, Amphipoda, Isopoda and Bivalvia were classified at practically the same contribution level in the three DCs. Thus, the main community structure differences related to depth were due to the higher contribution of Sipuncula, and Ostracoda in the UBZ compared to LBZ and AZ. Whereas, Harpacticoida showed a high contribution at the low bathyal, and abyssal stations and, the low one in UBZ. On the other hand, Tanaidacea, Porifera and Nemertea recorded a parabolic pattern. In LBZ the first two taxa recorded the highest contribution, while the latter registered the lowest one. Gastropoda, Cumacea, Scaphopoda and Pycnogonida were collected only in UBZ and LBZ sites while Brachiopoda only in AZ. Differences of these communities in a depth interval have been attributed to several factors. Among them, sediment grain size variations, oxygen availability (Etter and Grassle, 1992; Levin et al., 2001), organic carbon flux (Hernández-Ávila et al., 2021), and proximity to slope habitats (Woolley et al., 2016). In our analysis, the environmental factors related to faunal distribution were temperature, dissolved oxygen, PAHs, organic matter in SOGOM 3 and depth in SOGOM 4. All of them have been recorded as benthic community drivers in the deep sea (Cosson et al., 1997; Allen, 2008; Levin and Sibuet, 2012; Brown and Thatje, 2014; Bernardino et al., 2016; Brandt et al., 2018). The macrofauna communities difference between cruises observed in the multivariate analysis was mainly due to abundance variations as composition and structure were similar in both samplings.

4.4 Biodiversity estimates

The general alpha diversity depth-related pattern registered was similar in both cruises and according to the common pattern observed in the deep sea. Usually, the highest diversity values are registered in medium depths (2000-3000 m) and the lowest ones in the upper bathyal and abyssal regions (Rex, 1981; Ramirez-Llodra et al., 2010; Bernardino et al., 2016; Wei and Rowe, 2019). Some authors mention that high diversity in the LBZ may be due to UBZ and LBZ overlapping fauna (Levin et al., 2001; Snelgrove and Smith, 2002). The same trend has been recorded in the deep sea of the northern GoM region (Wei and Rowe, 2019). This could indicate that the processes that controling diversity in the benthic macrofauna could be similar throughout the Gulf. In our study, this pattern was consistent on the three estimated Hill numbers. Even though if a low taxonomic resolution was used, this bathymetric diversity macrofauna pattern of diversity was observed.

The diversity geographic pattern analysis showed that highest taxonomic diversity values of both cruises were located at medium depths in the southern and northwest regions of the study area. We also registered some sites with medium and high diversity values in the abyssal plain in both cruises. This region was usually characterized with low abundance but high diversity macrofauna. Dominance is not frequent, and it is very common to register a single specimen of each species (Sanders, 1968; Rex, 1981; Ramirez-Llodra et al., 2010). Organic matter accumulation is usually mentioned as one of the factors that could support high diversity and may be one of the reasons to explain high diversity values recorded in the Campeche and Coatzacoalcos Canyons. Finally, although the relationship between diversity and latitude is a phenomenon frequently recorded (Poore and Wilson, 1993; Rex et al., 1993; Gage, 2004; Rex et al., 2005), we did not observe a trend of geographic distribution diversity related to latitude in the southwestern Gulf of Mexico.

5 Conclusions

This study contributes with unique knowledge of macrofaunal communities in a large area and bathymetric range of the scarce studied area of southern GoM. UBZ presented different environmental conditions compared with LBZ and AZ. The UBZ was characterized by important DO concentrations, salinity, temperature variations, and high OM, silt, hydrocarbon values as well as low carbonate and clay sediment concentrations. On the other hand, LBZ and AZ presented high DO, salinity and temperature stability, low OM, hydrocarbons and silt values, high carbonate, and clay values in sediment. The high taxa registered are typical of deep sea macrofauna communities. The macrofauna abundance showed a depth related pattern. Highest abundance was registered in the south area at relatively low deep locations near the coast, whereas the lowest ones were found in the abyssal zone. The highest diversity was found in the south and northwest of the study area at medium depths. Even though the low taxonomic resolution level used, a community structure and diversity depth related pattern were recognized. Furthermore, there were differences between cruises in community abundance that can be related to seasonal abundance effect. Depth, water temperature, dissolved oxygen, OM and PAH in sediments were identified as the main drivers of macrofauna community structure. Data provided would be very important for understanding the GoM as whole and for assessing the impact of man driven activities such as accidental oil spills and/or long-term ecosystem changes.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

OQ-R: conceptualization, methodology, formal analysis, investigation, data curation, manuscript writing and visualization. ARV-B: conceptualization, methodology, manuscript writing, review and editing. AG conceptualization, methodology, investigation, resources, manuscript writing, review and editing, supervision, project administration, and funding acquisition. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling Editor SH declared a shared consortium CIGOM with the author AG at the time of review.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1033596/full#supplementary-material

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Title page

Title: Abundance and diversity patterns of Polychaeta families in the southwestern Gulf of Mexico deep waters

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Abstract:

Polychaetes larger than 500 micrometers collected from 63 sites in deepwater of the southwestern Gulf of Mexico were analyzed. Each site was sampled once a year during four consecutive years (2015-2018) with some exceptions. Sampling was carried out over a wide geographic area (92.67° to 96.70° W and 18.74° to 23.04° N) and in a large depth range (185 to 3749 m). A regional analysis was done with summed abundances related to the average of the environmental variables values recorded in each site during the four samplings. In addition, we performed a seasonal analysis between the last two cruises. The environmental variables measured in the bottom water showed important variations between 185 and 1000 m, but were remarkably stable in deeper zones. The abyssal region localities were characterized by high values of latitude, bottom water dissolved oxygen and carbonate content in sediments, whereas upper bathyal localities recorded high bottom water temperature, aromatic hydrocarbons, organic matter and silt concentration values. A total of 1968 specimens belonging to 45 polychaete families were collected. The most abundant families were: Spionidae, Paraonidae, Capitellidae, Cirratulidae, Amphinomidae, Opheliidae, Pilargidae, Lumbrineridae, Longosomatidae and Glyceridae. These families contributed 70% of the total abundance. The more frequent families present in at least 41 sampling sites were: Cirratulidae, Capitellidae, Paraonidae, Spionidae and Opheliidae. The abundance registered a depth-related pattern with the highest values in shallow sites in the southern region near the coastline. The lowest abundance values were recorded in the northern region, particularly in the abyssal plain. Multivariate analysis showed depth-related changes in the polychaete community structure. Latitude, dissolved oxygen and organic matter were the main polychaete community drivers. The highest taxonomic diversity was recorded at intermediate depths, in the Campeche Bay salt domes zone besides, some sites located in the northeast, and southeast regions and in the abyssal zone. The seasonal analysis showed variations in the sediment composition between cruises, but we did not register significant differences in abundance between cruises neither when comparing each SOGOM 3 DC with its respective SOGOM 4 DC. The taxonomic composition was very similar between SOGOM 3 and SOGOM 4 cruises. Thirty-six families were registered in both samplings and only four were exclusive to each of them. The dominant families were similar in both samplings. Nine of the ten most abundant families were the same in both cruises. The most related abiotic variables with fauna distribution were latitude, longitude and aromatic hidrocarbons during SOGOM 3, and latitude, longitude and alifatic hidrocarbons during SOGOM 4.

Key words: Deep sea, Polychaeta, Gulf of Mexico, abundance, macrofauna, diversity

1. Introduction:

The deep sea, from 200 m depth up (Fiege et al., 2010; Gage and Tyler, 1991), has particular characteristics like high hydrostatic pressure, light absence, low temperature and scarce and intermittent food availability (Danovaro et al., 2014; Ramirez-Llodra et al., 2010). It represents 90% of the world oceans area where soft sediments dominate (Gage and Tyler, 1991; Gray, 2002). The macrofauna is an important component of the infaunal communities that inhabit the soft bottoms. It is composed of metazoans under 1.5 cm length that are retained in a sieve with a mesh size between 250 and 500 micrometers (Gage, 2001; Hessler and Jumars, 1974; Rex, 1981; Rex et al., 2006). These communities are dominated by polychaete annelids, peracarid crustaceans and bivalve molluscs (Gage, 2001; Levin and Gooday, 2003; Rex et al., 2006). Polychaetes represent between 40 and 70% of the specimens recovered in a macrofauna sample (Glover et al., 2008; Jumars, 1975; Qu et al., 2016). Polychaetes are an important macrofauna component. They participate in biogeochemical cycles, ecological interactions and environment transformation where they live. This taxon plays an essential role in sustaining the deep-sea and the global ocean ecosystems (Hutchings, 1998; Magalhães and Barros, 2011; Pagliosa, 2005). Besides, polychaetes by themselves are good key indicators to evaluate the state of the environment they inhabit (Grassle and Maciolek, 1992; Olsgard et al., 2003; Olsgard and Somerfield, 2000).

The first studies of deep sea polychaetes were fundamentally taxonomic. In 1872, the year the Challenger expedition began, Sars G. and Sars M., father and son, reported 427 species, among them polychaetes, collected between 200 and 300 fathoms (350-550 m) (Sars and Sars, 1872). Expeditions such as Challenger carried out between 1872 and 1876 (McIntosh, 1885) followed by other very important ones: Talisman (France), Albatross (USA) and Galathea (Denmark) among others (Gage and Tyler, 1991) provided the first biological material from this environment. Among the first authors who studied deep sea polychaetes, Olga Hartman made a great contribution studying specimens obtained during the Allan Hancock expeditions (Hartman, 1963, 1960) and the Atlantis expeditions in the Northwest Atlantic (Hartman and Fauchald, 1971). Also important are the contributions made by Kirkegaard and Holthe of the Galathea expeditions (Holthe, 2000; Kirkegaard, 1996). Since then, the effort has continued fundamentally on a regional basis (e.g., Aguirrezabalaga and Gil, 2009; Alalykina, 2018; Glover et al., 2001).

In the deep sea of the northern Gulf of Mexico, multiple studies on polychaete communities were carried out (Carvalho et al., 2013; Qu et al., 2017, 2016; Reuscher and Shirley, 2017; Stuart et al., 2017) that allowed to identify the sites of highest abundance and diversity located in this region (Qu et al., 2016). However, in the Exclusive Economic Zone of Mexico deep waters, the knowledge of these communities is comparatively minor (but see Pérez-Mendoza et al., 2003; Quintanar-Retama et al., 2022). Recently a large number of studies have been conducted as part of international and mexican collaborative initiatives in the southern GoM to assess its environmental and biological conditions with regard to ecological impacts related to potential large oil spills derived from hydrocarbon exploration and exploitation activities in deep waters of this region (Murawski et al., 2020; Pulster et al., 2020; Reuscher et al., 2020; Schwing et al., 2020). In this context, the present study had the following objectives: i) to analyze composition of the polychaete communities of the benthic macrofauna at family taxonomic level; ii) to determine their abundance and diversity patterns and iii) to assess the environmental variables most related to these communities distribution in the deep sea of the southwestern GoM.

2. Materials and methods

2.1 Study area

The Gulf of Mexico is one of the most productive and diverse Large Marine Ecosystems of the world (Kumpf et al., 1999) bordered by three nations (US, Cuba, and Mexico). It has an area of about 1,540,000 km^2 (Ward and Tunnell, 2017) and a maximum depth near to 4000 m in the central area and the Sigsbee Canyon (Darnell, 2015). Most of the GoM (65%) are deep waters of which 42% corresponds to continental slope (200-3000 m) and 24% to abyssal plains (> 3000m) (Ward and Tunnell, 2017). More than a half of its surface area (55%) is Mexican Economic Exclusive Zone. Deep Gulf bottoms are mainly composed of mud from terrigenous and biogenic origin. The Loop Current from the Caribbean Sea determines the Gulf circulation pattern. This current enters through the Yucatán Channel and leaves through the Florida Straits and produces several cyclonic-anticyclonic gyres of different scales depending on the wind and pressure effects (Monreal-Gómez and Salas-de-León, 1997). A general net current flows in a West-North-East direction around the Gulf from Campeche Bank to Florida (Monreal-Gómez et al., 2004). Freshwater is discharged by several rivers around the Gulf among them the Mississippi River in the North and the Grijalva-Usumacinta River System in the South contribute with the highest load.

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 southwest of the GoM during oceanographic cruises SOGOM 1 to SOGOM 4 carried out from June 3–27, 2015; August 31 to September 20, 2016; April 21 to May 15, 2017, and from August 29 to September 20, 2018, respectively. The sampling sites were located within a geographic range of 92.67°–96.70° West longitude and 18.74°–23.04° North latitude, in a depth range of 185 to 3749 m (Fig. 1). The sampling design considered 63 locations on each cruise; however, due to logistical reasons only 60, 62, 56 and 62 were successfully sampled from SOGOM 1 to SOGOM 4, respectively. The original numbering of each site was retained for cross-cruise comparisons.

The sediment was collected with a Reineck-type box corer of 0.16 m^2 effective area. A sediment sample of 0.08 m^2 surface and 13 cm depth was collected for faunal analysis in each core. Faunal samples were sieved on board with filtered seawater through a mesh of 500 µm size. The taxonomic identification was done using general taxonomic literature (e.g. De León-González et al., 2009; Fauchald, 1977). Only identified fauna was included in the analysis. A more detailed description of the sampling and sample processing methodology can be found in Quintanar-Retama et al., (2022, 2023).

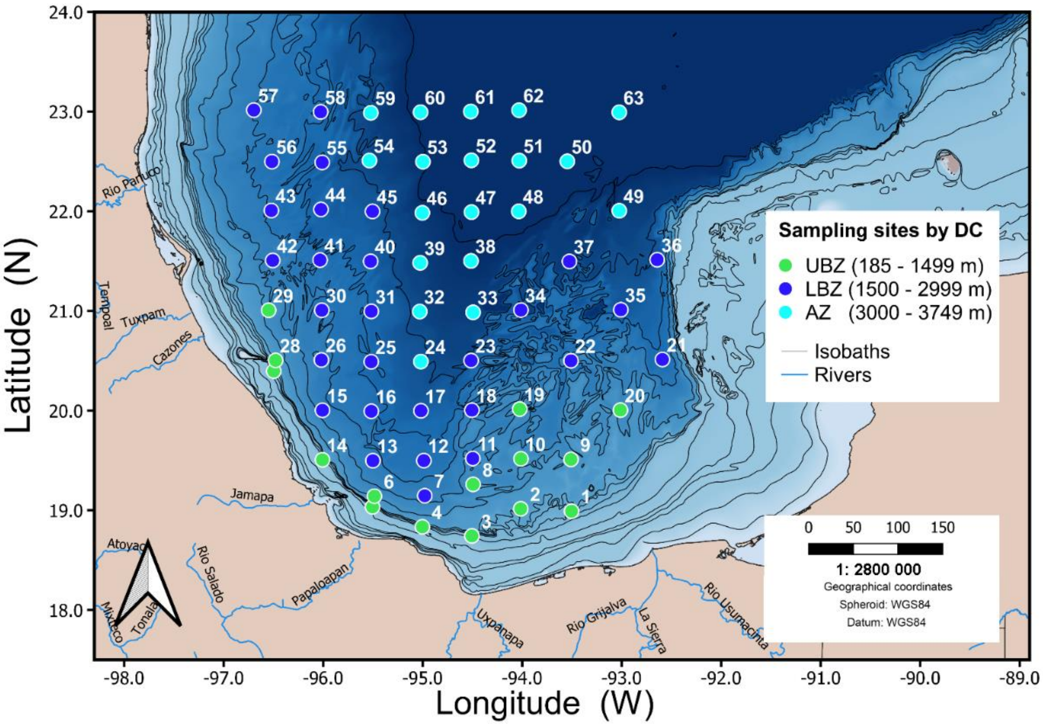


Figure 1. Location of the 63 sampling sites in the oceanographic cruises SOGOM 1-4 Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

2.3 Data analysis

The data analysis was carried out as follow: first, a regional analysis was performed. For the faunal matrix, the counts recorded at each site during the four cruises were added and standardized at ind. m-^{2}. For the environmental factors analysis, the average of the values obtained in each site was calculated. Second, a temporal analysis was carried out. Only cruises 3 and 4 were considered for this analysis because we observed very low abundances during SOGOM 1 (202 specimens) and SOGOM 2 (174 specimens) compared to 3 and 4 (856 and 736 specimens, respectively). In addition, in the samples of the first two cruises we found abundant animal fragments and many specimens could not be identified due to their poor conservation state. Therefore, the temporal analysis was performed comparing only cruises 3 and 4 to avoid possible bias due to the abundance underestimation in the first two samplings. The abundance values recorded at each site also were standardized to ind. m^{-2} in both cruises.

We established the limit between bathyal and abyssal regions at 3000 m according to the literature (e.g.,Harris, 2020; Watling et al., 2013) and the GoM bathymetry.Then, the sampling sites were organized in three depth categories (DC): upper bathyal zone (UBZ, 185–1500 m), lower bathyal zone (LBZ, 1501–3000 m), and abyssal zone (AZ, 3001–3749 m).

We made a correlation analysis among the environmental variables to determine which of them covaried. In order to reduce the dimensionality and assess which of the environmental factors could be characterizing each depth category, a principal component analysis was carried out from the environmental variables normalized matrix (removing those that covaried). This was made with R software (R Core Team, 2022). For the visualization results we used the pheatmap and factoextra libraries (Kassambara and Mundt, 2020; Kolde, 2019). Average, and registered values in each site were used for the regional and temporal analyses respectively.

We also made a smooth line plot for each environmental variable for the regional and seasonal analysis that included the value registered in each site for each cruise and the average per site with a 0.3 span and sites ordering by depth. Also, Kruskal-Wallis tests were carried out to determine the significant of possible differences between cruises in the seasonal analysis. Besides, based on the standardized abundance matrices, we constructed box plots to assess possible variations in abundance between DC in the regional analysis and between cruises and DC in the temporal analysis. Kruskal-Wallis tests were realized to assess the significance of the abundance across cruises and/or depth zones. In addition, we constructed percentage and basic stacked bar charts to analyze site-specific bathymetric changes in standardized and relative polychaete abundance. The significance between depth and abundance relationship was evaluated with Spearman’s correlation. These were carried out with ggplo2 and ggpubr libraries (Kassambara, 2020; Wickham, 2016) in R.

We elaborated a non-metric multidimensional scaling (nMDS) from pairwise similarity matrix between sites based on the Bray-Curtis index (Clarke et al., 2014) based on square root transformed standardized abundance matrices. Also from similarity matrix we did a hierarchical classification analysis (group average) including SIMPROF test (1000 permutations for average profile, 999 simulation permutations and 5% level of significance). This were plotted on each ordination obtained through the nMDS. The libraries used for this were: vegan, ggplot2, and clustsig (Oksanen et al., 2022; Whitaker and Christman, 2014; Wickham, 2016) in R.

Spearman correlations (RS) between biotic and abiotic similarity matrices were estimated using the BIOENV routine (Clarke et al., 2008) with vegan library (Oksanen et al., 2022) in R. The analysis included nine environmental factors (latitude, longitude, depth, temperature, dissolved oxygen, polycyclic aromatic hydrocarbons, aliphatic hydrocarbons, organic matter and silt). Each similarity matrix of abiotic factors was made by Euclidean distances of the environmental variables normalized matrix. Also, we made heat maps to show the possible variations in the polychaete communities composition and structure among DC with the pheatmap library (Kolde, 2019) in R.

We compute diversity estimates (Hill numbers) of order q = 0, 1, and 2 with the iNEXT library (Chao et al., 2014) in R, and constructed continuous extrapolation and rarefaction sampling curves for each one of them. Maps of abundance and diversity values distribution was done.

3. Results

3.1 Regional results

3.1.1 Regional environmental analysis

Principal component analysis showed that latitude, organic matter, aromatic hydrocarbons and carbonate concentration in sediments were the environmental variables most related to component one, while longitude and aliphatic hydrocarbons in sediments were the abiotic factors most related to component two. Both components registered 70% of the observed variability. Sites were ordered in a bathymetric gradient in which the abyssal region localities were characterized by high latitude, and high values of bottom water dissolved oxygen and carbonate content in sediments. On the other hand, localities in the upper bathyal region were characterized by high bottom water temperature, aromatic hydrocarbons, organic matter and silt concentration values (Fig. 2).

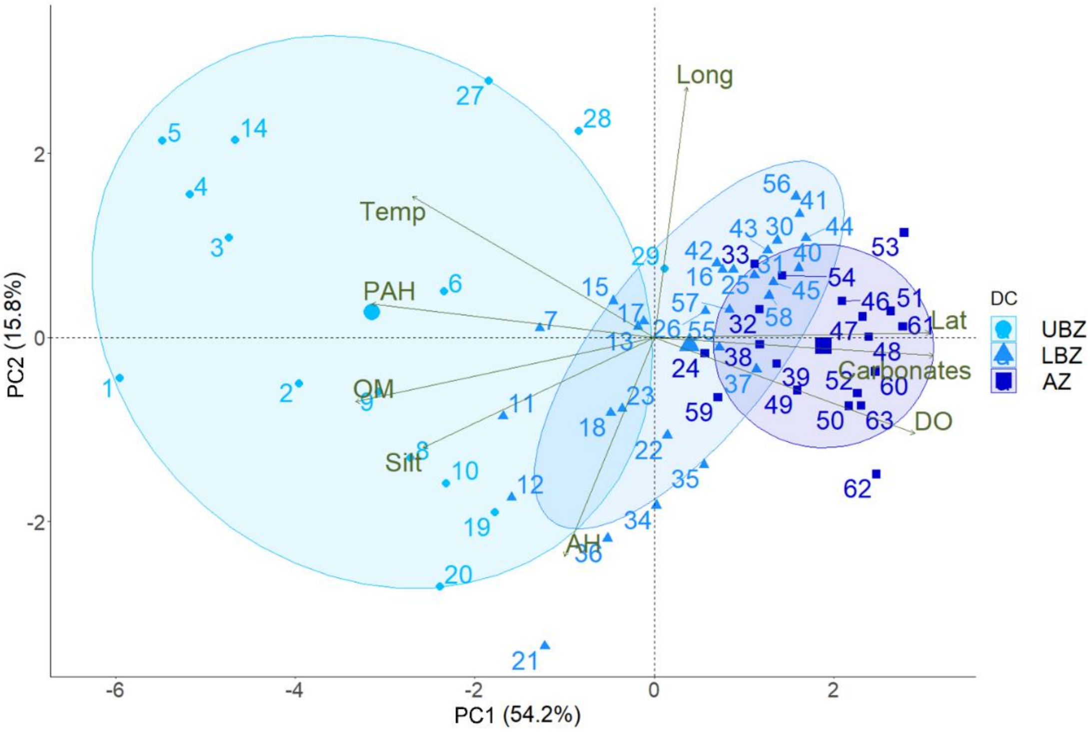


Fig. 2. Two-dimensional PCA ordinations on the environmental variables of SOGOM 1-4 (PC1 and PC2 accounted for 70% of the variation). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

Salinity and temperature did not present important variations among the four cruises. Temperature varied from 18.3 to 4.6 °C among 185 and 1465 m depth and was always close to 4 °C at deeper sites. Salinity records varied between 36.45 and 35.48 PSU in a 185 and 450 m depth range. At deeper locations, values were always close to 35 PSU. The dissolved oxygen values were generally recorded within a range of 2.21 to 3.93 ml l^{-1} at 185-1508 m depth range, with exception of site 29 where we registered 4.25 ml l^{-1}. In deeper locations, dissolved oxygen values showed a range from 3.98 to 4.43 ml l^{-1} with an average of 4.28 ml l-1. Dissolved oxygen concentration was consistently lower in SOGOM 1 than the other three cruises. (Supplementary data).

The OM, carbonate, silt and clay content in sediments were very similar among samplings except the silt and clay values recorded during SOGOM 3 and 4. In this sense, we observed that the silt values were lower in LBZ and clay was higher in AZ during SOGOM 4 compared to the other cruises. The organic matter and silt concentrations showed a decreasing pattern related to depth, while the carbonate and clay values showed an opposite trend increasing with depth. The OM and carbonates values were recorded in intervals from 1.2 to 3.0% and from 8.4 to 23.5%, respectively. Whereas silt and clay values varied between 54% and 79%, and from 21% to 46% respectively. Aromatic hydrocarbons increased progressively from SOGOM 1 to SOGOM 4 practically at all sites in the analyzed depth profile. We observed the same pattern in the aliphatic hydrocarbon registers. However, in this case SOGOM 3 recorded the highest values followed by SOGOM 4. Highest aromatic hydrocarbon values were registered in UBZ and the lowest in LBZ and AZ. Aliphatic hydrocarbons presented similar values throughout the analyzed depth range with relatively high values in sites greater than 2500 m depth. The aromatic hydrocarbon values were recorded in a range from 51 to 115 µg/kg. While, the aliphatic hydrocarbons values were observed between 1166 and 2947 µg/kg. (Supplementary data).

3.1.2 Regional faunal description

The number of the sites grouped in the UBZ, LBZ, and AZ was: 15, 29, and 19, respectively. The number of specimens in each DC was: 977, 698 and 293 while the number of families was: 40, 41 and 30 also, respectively (Table 1).

Table 1.
Number of sites, specimens and families, average abundance and depth for each depth category.

SOGOM 1-4

Depth category	Number of sites	Number of specimens	Number of families	Average abundance (ind. m^{-2})	Average depth (m)
UBZ	15	977	40	239 (range: 94 -583)	753 (range: 186 -1466)
LBZ	29	698	41	95 (range: 29 - 333)	2293 (range: 1508 - 2545)
AZ	19	293	30	65 (range: 9- 238)	3441 (range: 3018- 3749)

We collected 1968 specimens belonging to 45 polychaete families (Supplementary data). The ten most abundant families were: Spionidae, Paraonidae, Capitellidae, Cirratulidae, Amphinomidae, Opheliidae, Pilargidae, Lumbrineridae, Longosomatidae and Glyceridae in order of abundance and accounted for 70% of the total relative abundance (Fig. 3). The most frequent families were Cirratulidae, Capitellidae, Paraonidae, Spionidae and Opheliidae collected in 54, 52, 51, 47 and 41 sampling sites, respectively. On the other hand, the families with a single record and only one specimen collected were: Sabellariidae, Sphaerodoridae, Pectinariidae, Serpulidae, and Travisiidae. Uncispionidae was also registered in one site but with three specimens. (Supplementary data).

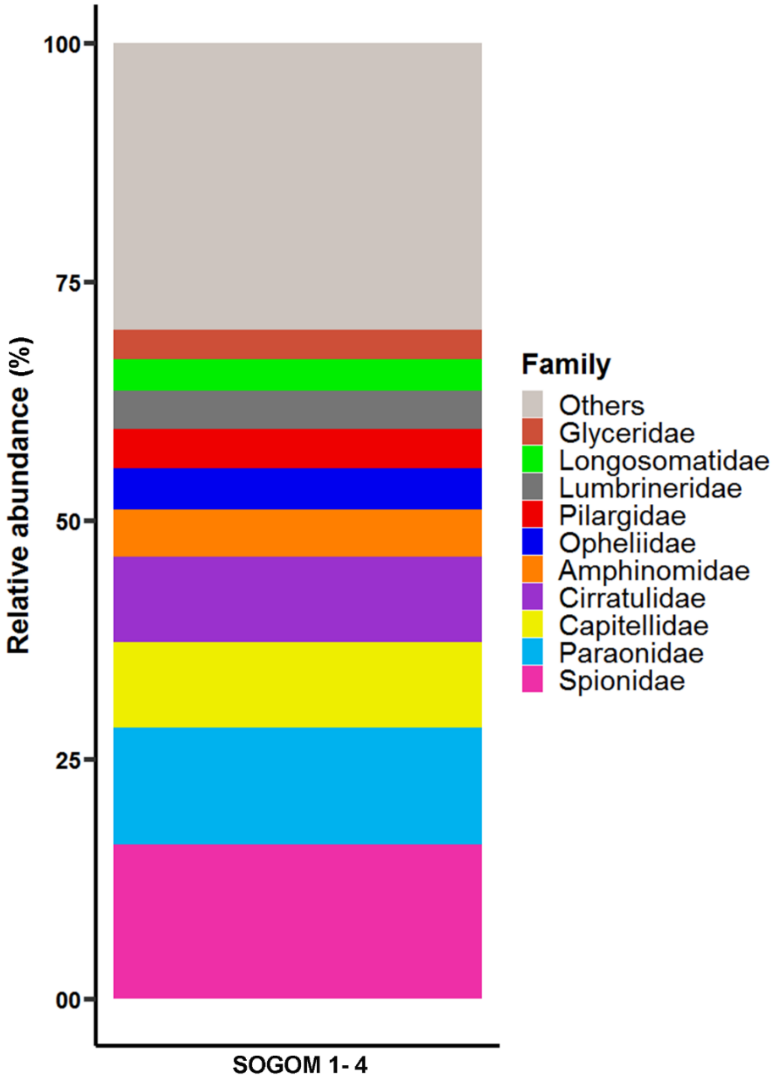
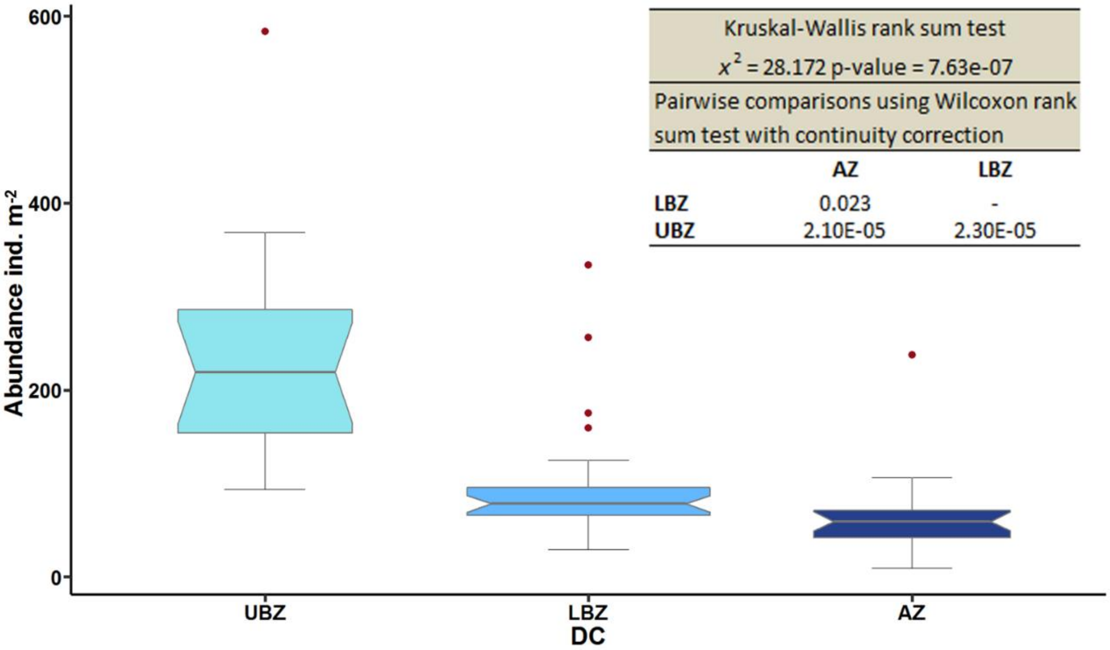


Figure 3. Relative abundance of the ten most abundant polychaete families of SOGOM 1-4.

The standardized average abundance was 120 ind. m^{-2} in a range of 9 ind. m^{-2} (site 61 in the northeast region at 3727 m depth) to 583 ind. m^{-2} (site 14 in the southern region at 186 m depth). In general, we observed a decrease of abundance with increasing depth (Figs. 4 and 5). Interestingly five sites (7, 18, 23, 32 and 34) registered higher abundance values than adjacent sites in the bathymetric profile (Fig. 5).



Kruskal-Wallis rank sum test

x^2 = 28.172 p-value = 7.63e-07

Pairwise comparisons using Wilcoxon rank sum test with continuity correction

	AZ	LBZ
LBZ	0.023	-
UBZ	2.10E-05	2.30E-05

Figure 4. Box plot of polychaete abundance (ind. m^{-2}) registered in SOGOM 1-4 in each DC. Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

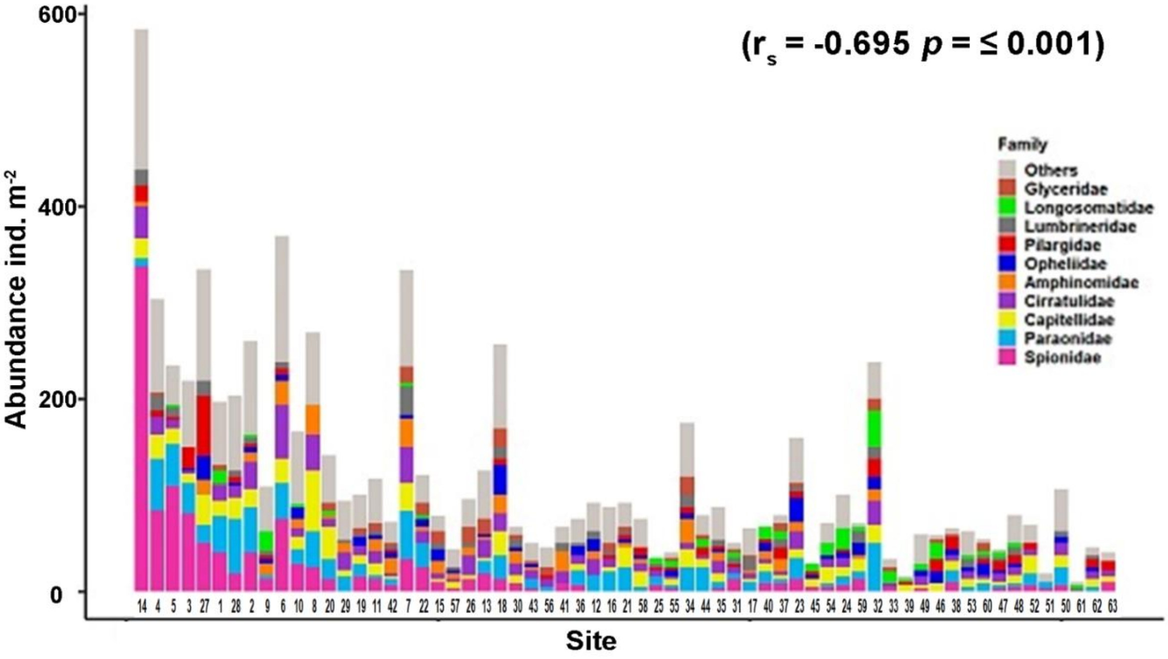


Figure 5. Abundance of polychaete families related to depth SOGOM 1-4. Sites were ordered from left to right from shallowest to deepest.

In general, the highest abundance values were recorded in the south of the study area in locations near to the coastline and the lowest ones in the northern region sites. Intermediate values were also associated with southern locations near to the coastline besides sites located in the Campeche Bay salt domes zone and in the continental rise. The lowest abundance values were recorded in all regions of the study area, particularly in the abyssal plain in the northern region (Fig. 6).

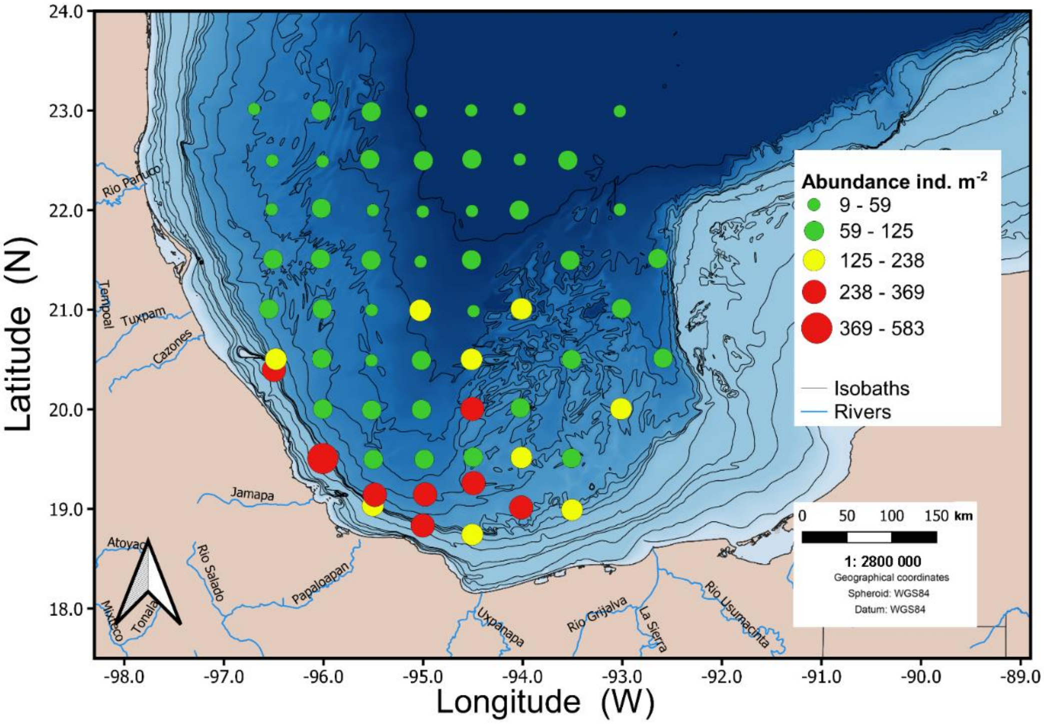


Figure 6. Spatial distribution of the polychaete abundance values during SOGOM 1-4.

3.1.3 Regional multivariate analysis

The nMDS showed depth- related changes in the polychaete community composition and structure. Even though each group did not separate categorically from each other, a gradual bathymetric change was observed (Fig. 7a).

The cluster analysis with the SIMPROF test confirmed this depth-related community pattern with a high similarity between the LBZ and AZ fauna. The sites were grouped into nine clusters. Three groups (1, 2 and 9) included sites from the abyssal region. Another three (5, 6, and 7) from the UBZ. Two groups (3 and 4) contained sites from LBZ. The biggest group was the number eight with two sites from UBZ and most of them from LBZ and AZ (Fig. 7b and Supplementary material). The ANOSIM analysis also agrees with these results. The global value was relatively low 0.287 but significant (*p* = 0.001). However, the comparison between pairs allowed us to observe the gradual change in the analyzed depth range.

rANOSIM was 0.3 between LBZ and UBZ, 0.16 between LBZ and AZ and 0.49 between UBZ with AZ (*p* = 0.001 in the three cases).

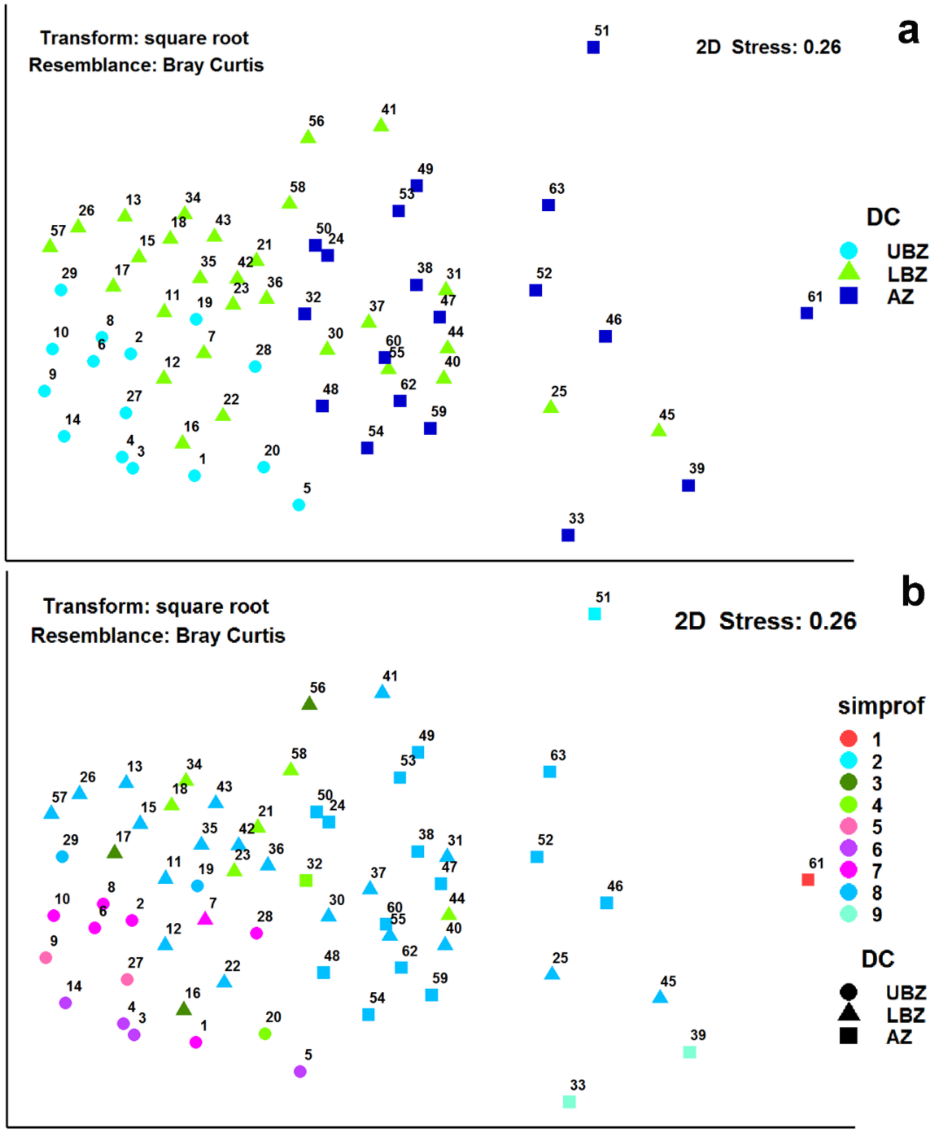


Figure 7 a-b. a) Non-metric multidimensional scaling of the polychaete communities of SOGOM 1-4 based on Bray Curtis similarities. Upper bathyal zone (UBZ- blue circle), lower bathyal zone (LBZ-green triangles) and abyssal zone (AZ-blue square). **b)** Same ordering with a classification analysis plotted.

The main bathymetric changes in the polychaete community structure were due to the high relative abundance of spionids registered up to 1200 m depth. Glycerids and amphinomids were more abundant between 1000 and 2500 m. whereas, ophelids and lumbrinerids recorded higher abundance from 1400 and 1700 m to the AZ, respectively. Pylargids and longosomatids were better represented from 2380 to

2550 m, respectively, and continued as important families until the deepest zone sampled. Paraonids and cirratulids registered a rather constant contribution to abundance along the bathymetric profile (Fig.8).

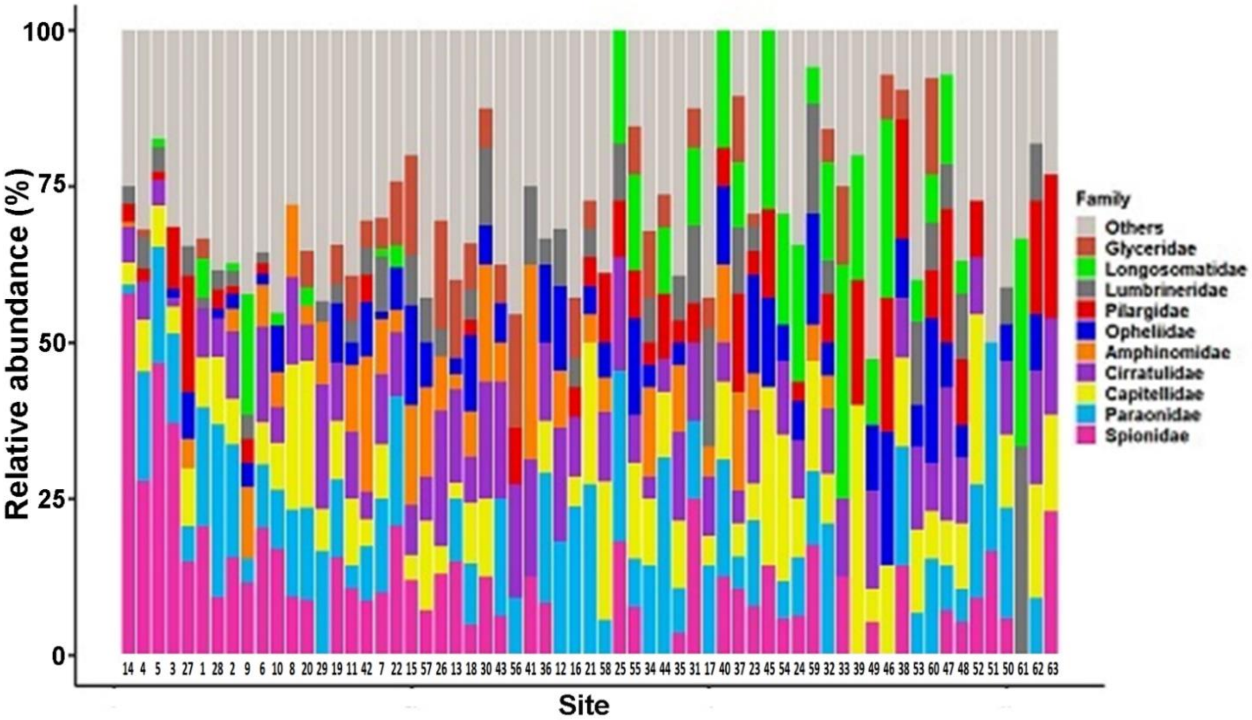
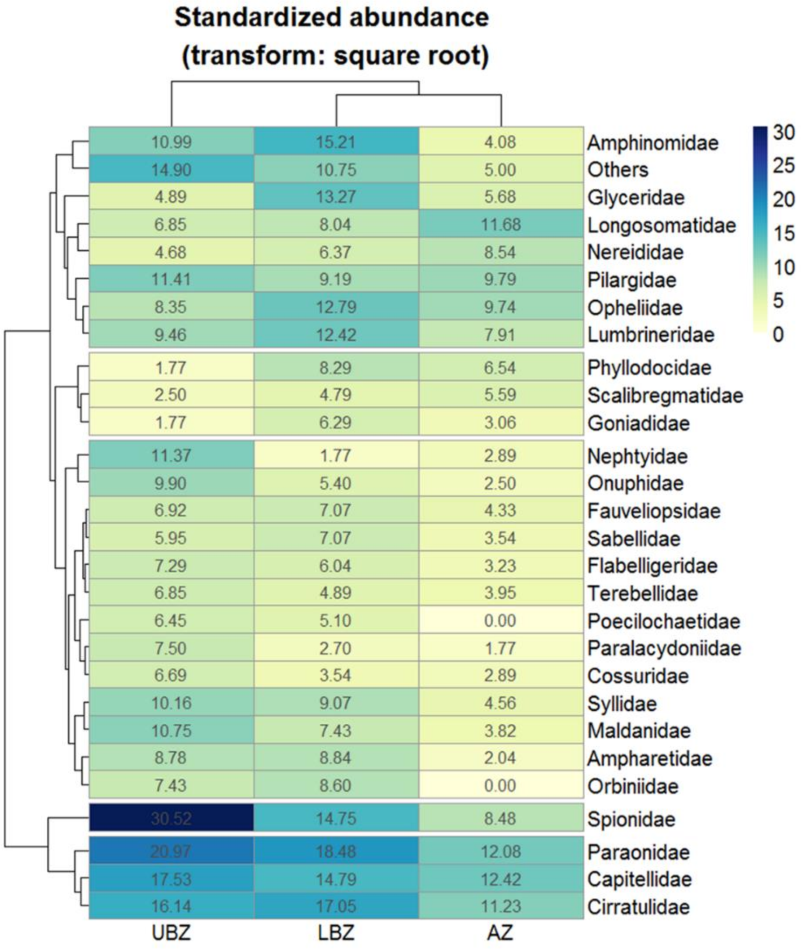


Figure 8. Relative abundance of polychaete families related to depth during SOGOM 1-4. Sites were ordered from left to right from shallowest to deepest.

The heatmap analysis revealed the variations of the polychaete community structure along DC considering the standardized abundance. The abundance of the Spionidae, Paraonidae, Capitellidae and Cirratulidae (the families that mainly contributed the most to the general abundance) decreased markedly with increasing depth, especially for the Spionidae. Lumbrineridae recorded their highest abundance at intermediate depths (LBZ), whereas Longosomatidae and Nereididae registered their highest abundance in AZ (Fig. 9).


Standardized abundance (transform: square root)

UBZ	LBZ	AZ	
10.99	15.21	4.08	Amphinomidae
14.90	10.75	5.00	Others
4.89	13.27	5.68	Glyceridae
6.85	8.04	11.68	Longosomatidae
4.68	6.37	8.54	Nereididae
11.41	9.19	9.79	Pilargidae
8.35	12.79	9.74	Opheliidae
9.46	12.42	7.91	Lumbrineridae
1.77	8.29	6.54	Phyllodocidae
2.50	4.79	5.59	Scalibregmatidae
1.77	6.29	3.06	Goniadidae
11.37	1.77	2.89	Nephtyidae
9.90	5.40	2.50	Onuphidae
6.92	7.07	4.33	Fauveliopsidae
5.95	7.07	3.54	Sabellidae
7.29	6.04	3.23	Flabelligeridae
6.85	4.89	3.95	Terebellidae
6.45	5.10	0.00	Poecilochaetidae
7.50	2.70	1.77	Paralacydoniidae
6.69	3.54	2.89	Cossuridae
10.16	9.07	4.56	Syllidae
10.75	7.43	3.82	Maldanidae
8.78	8.84	2.04	Ampharetidae
7.43	8.60	0.00	Orbiniidae
30.52	14.75	8.48	Spionidae
20.97	18.48	12.08	Paraonidae
17.53	14.79	12.42	Capitellidae
16.14	17.05	11.23	Cirratulidae

Figure 9. Heatmap of the abundance of polychaete families during SOGOM 1-4. Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

The BIOENV analysis indicated the principal polychaete community drivers. The environmental parameter combination (up to 3 factors) that showed the best match with biotic similarity matrix using the Spearman rank correlation were latitude, dissolved oxygen and organic matter with a 0.34 correlation (*p* = 0.002) with one permuted statistic greater than Rho (Supplementary data).

3.1.4 Regional analysis of diversity estimators

In the diversity analysis we recorded a 0.99 sampling coverage for the three DC. The coverage-based R/E (rarefaction and extrapolation) sampling curves showed LBZ as the DC with the greatest diversity for the three estimators calculated (Hill numbers, *q* = 0, 1 and 2) (Fig. 10).

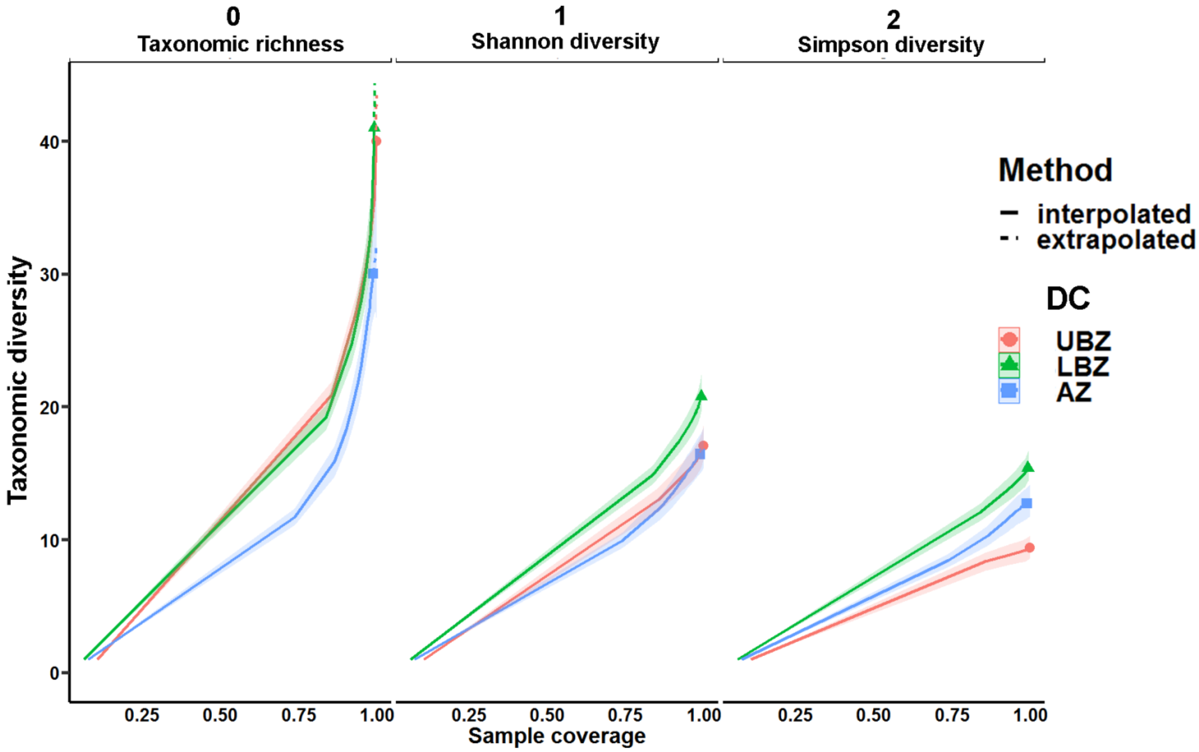


Figure 10. Coverage-based R/E (rarefaction and extrapolation) sampling curves for three Hill numbers (*q* = 0, 1, and 2). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

In general, we observed low diversity values in almost the entire study area, except for the Campeche Bay salt domes zone and Campeche Canyon where most of the sites registered intermediate and high diversity values. Some sites in the northeastern, southeastern, and abyssal plain regions also recorded intermediate and high diversity values (Fig. 11).

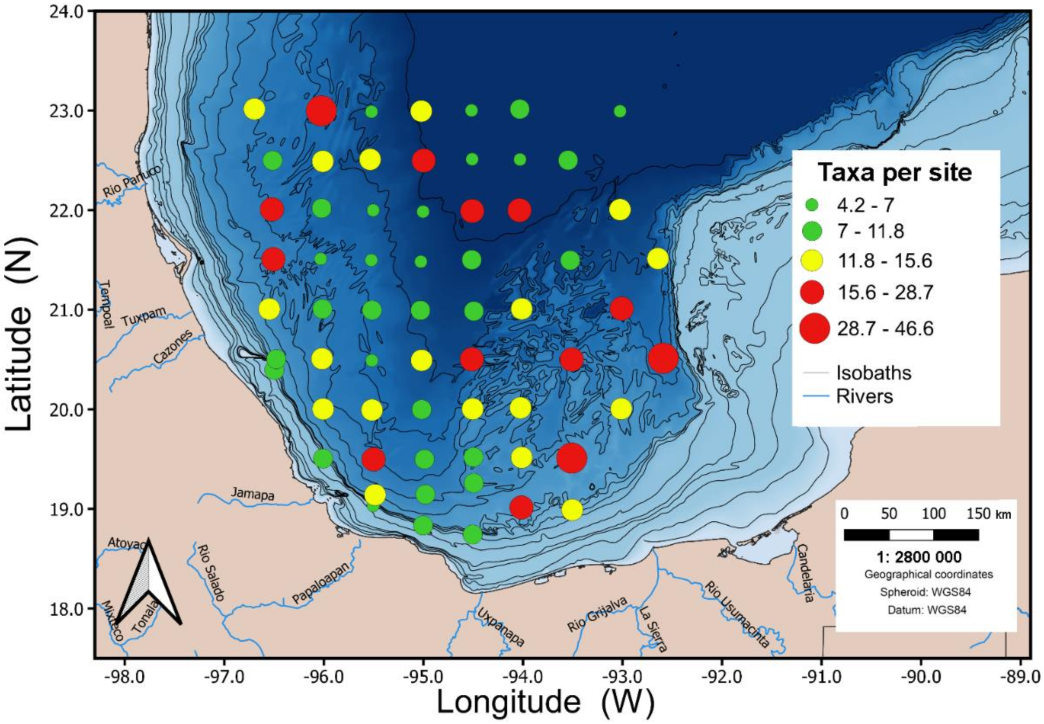


Figure 11. Spatial distribution of the polychaete diversity during SOGOM 1-4.

3.2. Seasonal results

3.2.1 Seasonal environmental analysis

The comparison between SOGOM 3 (April 21-May 15, 2017) and SOGOM 4 (August 29-September 20, 2018) (Supplementary data) made to evaluate the possible seasonality effect showed the same general trends that we reported for the regional analysis in all abiotic factors. The principal component analysis showed that latitude and organic matter were the environmental variables most related to component one besides aromatic hydrocarbons in SOGOM 3, and carbonate in SOGOM 4. Longitude and aliphatic hydrocarbons were the most related factors to component two in both cruises. Both components accounted for 67.8% and 63.9% of the observed variability during SOGOM 3 and SOGOM 4, respectively. The ordering of the sites in the PCA of SOGOM 3 and SOGOM 4 was similar to that registered in the regional analysis. The sites were ordered in a bathymetric gradient in which the abyssal region localities were characterized by higher latitude, dissolved oxygen and carbonate values while, the upper bathyal region localities presented higher temperature and aromatic hydrocarbons, organic matter and silt values (Fig. 12 a-b).

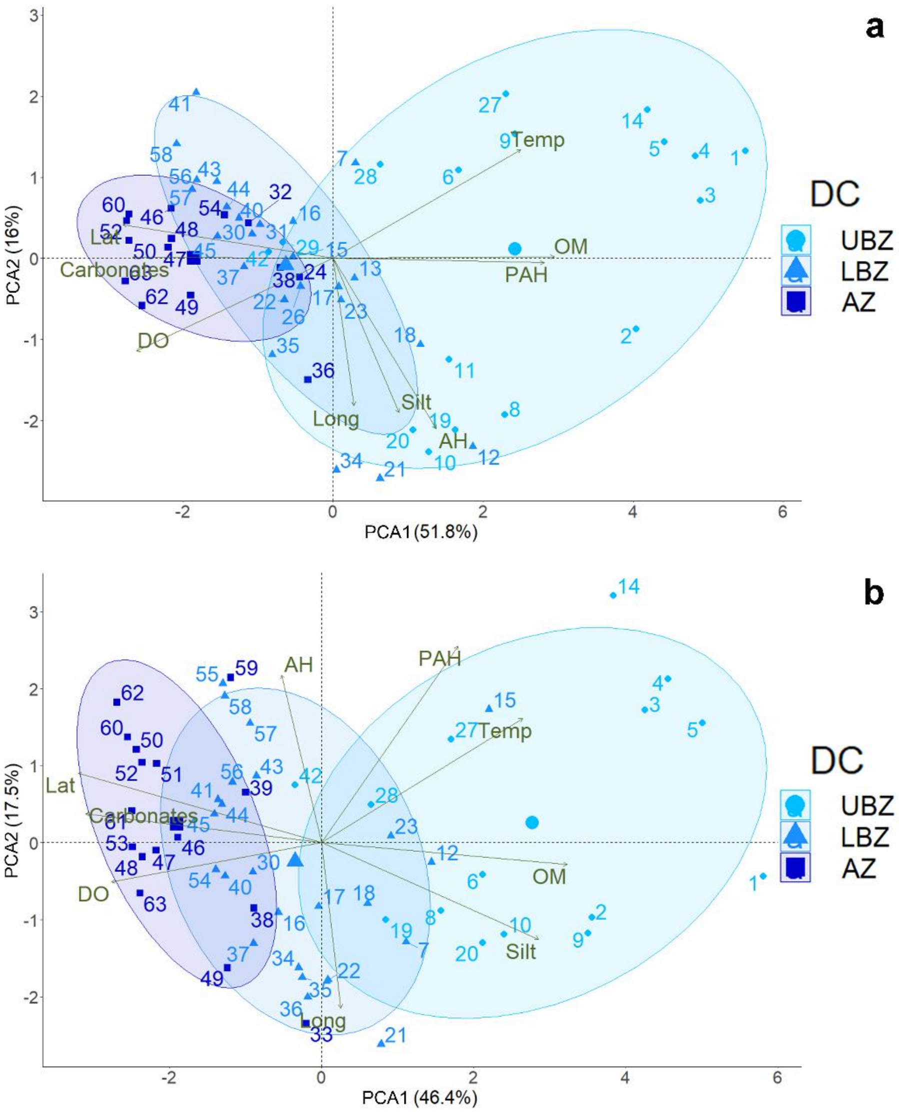


Figure 12 a-b. a) Two-dimensional PCA ordinations on the environmental variables of SOGOM 3 (PC1 and PC2 accounted for 67.8 % of the variation). **b)** Same analysis from SOGOM 4 (PC1 and PC2 accounted for 63.9% of the variation). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

In the comparison between cruises, we observed significant differences in eight abiotic factors. Salinity consistently registered higher values ($p \leq 0.001$) during SOGOM 3 (average: 35.20 PSU) compared to SOGOM 4 (average: 35.09 PSU). The average temperature value was lower in SOGOM 3 (5.51 °C) compared to SOGOM 4 (5.70 °C) ($p \leq 0.001$). Oxygen also showed significant differences between cruises ($p \leq 0.001$). The highest values were recorded during SOGOM 4. Latitude, longitude, and carbonate content did not show differences between cruises ($p = 0.898$, $p = 0.988$, $p = 0.890$, respectively) (Supplementary data).

Among the environmental variables measured in sediments, sand, silt, and clay showed significant differences between cruises (p = 0.034, p ≤ 0.001, p ≤ 0.001, respectively). The sand content value was zero at most sites in both cruises (45 sites during SOGOM 3, and 59 sites during SOGOM 4). The highest silt average value (65.5%) was recorded in SOGOM 3, while the highest of clay (40.1%) in SOGOM 4. We recorded a trend of increasing silt and decreasing clay content with increasing depth in the interval of 185 to 1000 m. In the rest of the depth range, both patterns were inverted; the silt trend was decreasing, and the clay trend was increasing in both cruises. We did not register difference between cruises in the OM content (p = 0.570). The average OM value was the same in both cruises 1.6%. Also, we observed that from 185 to 1500 m the highest values were recorded in SOGOM 3, from 1500 to 3000 m in SOGOM 4 and in the rest of the depth profile in SOGOM 3 again. The aromatic and aliphatic hydrocarbons also registered a significant difference between cruises (p ≤ 0.001 in both samplings). Aromatic hydrocarbons registered a higher average value during SOGOM 4 (88.5 µg/kg vs 72.3 µg/kg), while the aliphatic hydrocarbons presented a higher average value in SOGOM 3 (3205 µg/kg vs 2739 µg/kg) (Supplementary data).

3.2.2 Regional faunal analysis

During SOGOM 3, 17, 24 and 14 localities were successfully sampled and were grouped in the UBZ, LBZ and AZ regions, respectively. While the number of individuals collected in each of them were: 408, 295 and 153 and the registered families were 35, 34 and 26 also, respectively. During SOGOM 4 in UBZ, LBZ, and AZ we recorded 16, 28 and 18 localities, 395, 244 and 97 specimens and 37, 31, and 17 families, respectively (Table 2).

Table 2

Number of sites, specimens, and families. Average abundance and depth for each depth category of each cruise. Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

SOGOM 3

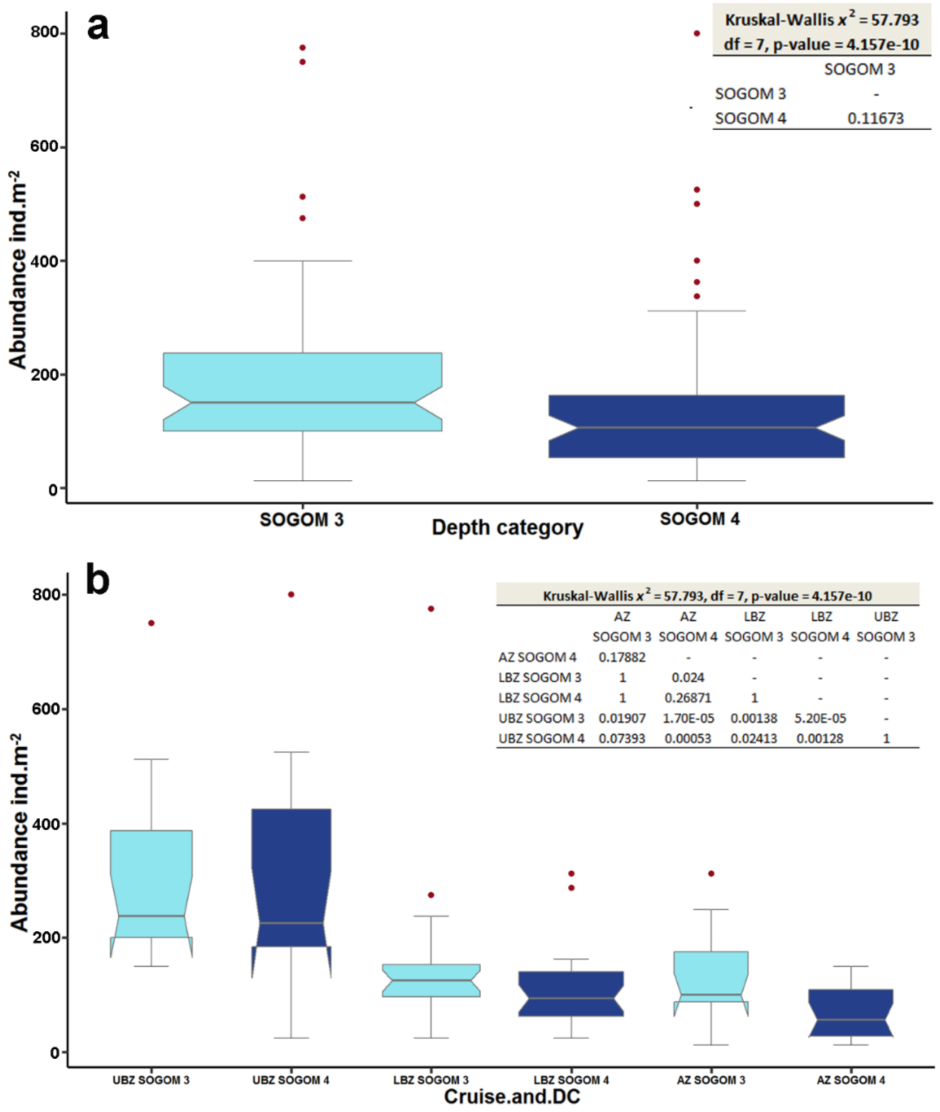
Depth category	Number of sites	Number of specimens	Number of taxa	Average abundance (ind. m^{-2})	Average depth (m)
UBZ	17	408	35	290 (range: 50 -750)	824 (range: 185 -1482)
LBZ	24	295	34	186 (range: 25 - 775)	2324 (range: 1629 - 2885)
AZ	14	153	26	134 (range: 13- 313)	3394 (range: 3001- 3740)

SOGOM 4

Depth category	Number of sites	Total specimens	Number of taxa	Average abundance (ind. m^{-2})	Average depth (m)

UBZ	16	395	37	309 (range: 25-800)	805 (range: 189-1467)
LBZ	28	244	31	109 (range: 25-313)	2449 (range: 2080-2875)
AZ	18	97	17	67 (range: 13-150)	3451 (range: 3027-3762)

The average polychaete standardized abundance was higher in SOGOM 3 (497 ind. m^{-2}, range: 125-1388) than in SOGOM 4 (347 ind. m^{-2}, range: 38- 1088), however this difference was not significant (Fig. 13 a). The comparison of each depth category of SOGOM 3 with their respective ones of SOGOM 4, neither showed significant differences. The analysis within each cruise of both samplings showed significant differences of UBZ abundance compared to LBZ and AZ. whereas no significant difference was found between LBZ and AZ (Fig. 13 b). The five most abundant polychaete families during SOGOM 3 were Spionidae, Paraonidae, Capitellidae, Cirratulidae, and Longosomatidae. These represented 46% of total abundance. These top four families together with Amphinomidae were the five most abundant taxa during SOGOM 4 and amounted 59% of the total abundance. The composition of the following five most abundant taxa was very similar between cruises. Opheliidae, Lumbrineridae, Pilargide and Glyceridae were found in both cruises, whereas Syllidae was registered only in SOGOM 4 and Amphinomidae in SOGOM 3 with lower ranking than in SOGOM 4 (Supplementary data). The families with the highest number of records were Spionidae and Paraonidae in both cruises besides Capiteliidae in SOGOM 3, and Cirratulidae in SOGOM 4.



Kruskal-Wallis x^2 = 57.793
df = 7, p-value = 4.157e-10

	SOGOM 3
SOGOM 3	-
SOGOM 4	0.11673

Kruskal-Wallis x^2 = 57.793, df = 7, p-value = 4.157e-10

	AZ SOGOM 3	AZ SOGOM 4	LBZ SOGOM 3	LBZ SOGOM 4	UBZ SOGOM 3
AZ SOGOM 4	0.17882	-	-	-	-
LBZ SOGOM 3	1	0.024	-	-	-
LBZ SOGOM 4	1	0.26871	1	-	-
UBZ SOGOM 3	0.01907	1.70E-05	0.00138	5.20E-05	-
UBZ SOGOM 4	0.07393	0.00053	0.02413	0.00128	1

Figure 13 a-b. **a)** Box plots of polychaete abundance (ind. m^{-2}) **a)** registered during SOGOM 3 and SOGOM 4, **b)** registered in SOGOM 3 (light blue) and SOGOM 4 (navy blue) in each depth category. Upper bathyal zone (UBZ), lower bathyal zone (LBZ), and abyssal zone (AZ).

Polychaete abundance presented a depth-related pattern decreasing when depth increased in both cruises (Figs. 13, b and 14 a-b). Some sites showed markedly higher abundances than adjacent sites in the depth profile. In SOGOM 3 they were sites 7, 23, 24, 32 and 36 (Fig. 14 a). While, in SOGOM 4 they were sites 20, 26, 13, 41 and 56 (Fig. 14 b).

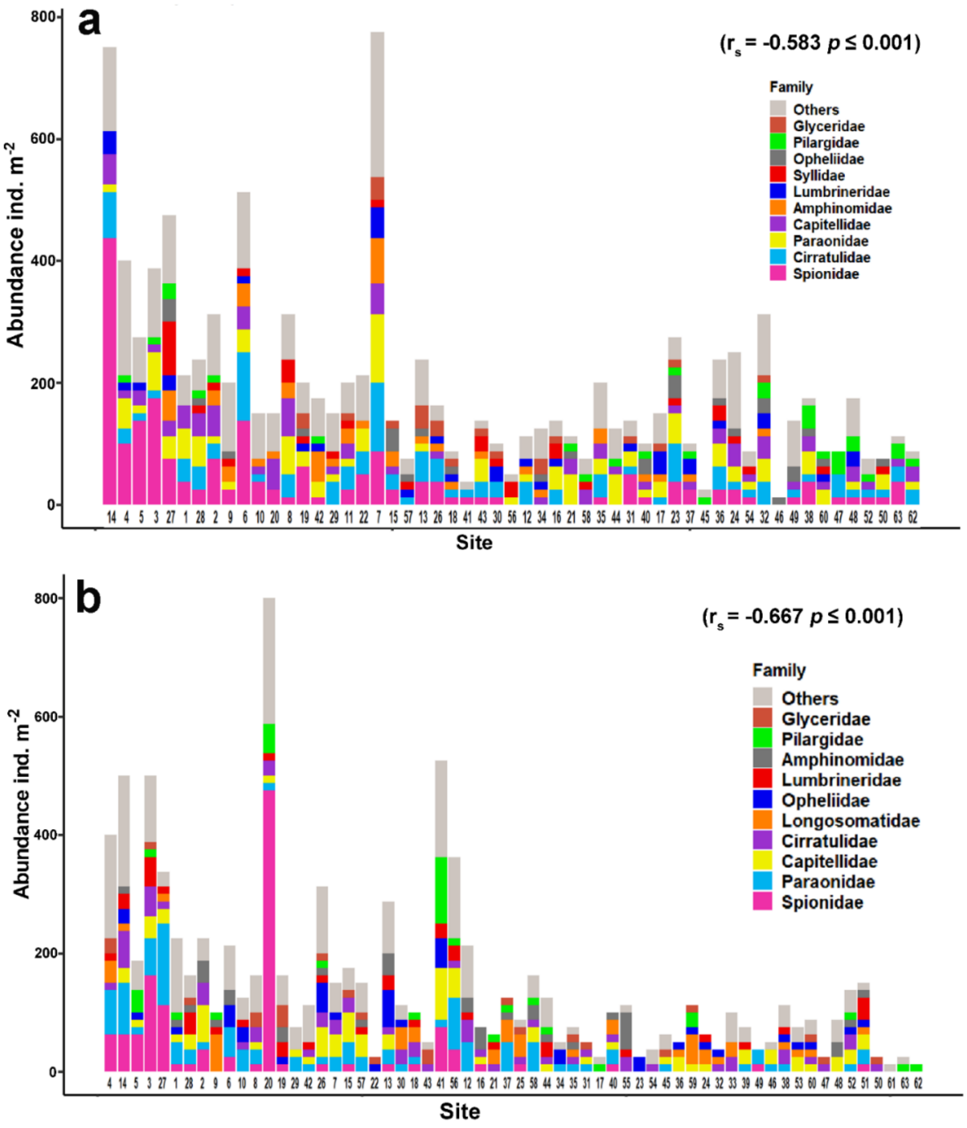


Figure 14 a-b. Abundance of polychaete families related to depth **a)** during SOGOM 3, **b)** during SOGOM 4. Sites were ordered from left to right from shallowest to deepest.

In the abundance spatial distribution, the southern and northwestern regions, as well as some sites in front of the mouth of the Tecolutla and Nautla rivers, remained as areas with intermediate and high abundance values in both cruises. Sites 8, 9, 10, 17 and 18 located in the salt dome zone of the Campeche Bay registered intermediate and high abundance values during SOGOM 3, and low values during SOGOM 4 (Fig. 15 a-b).

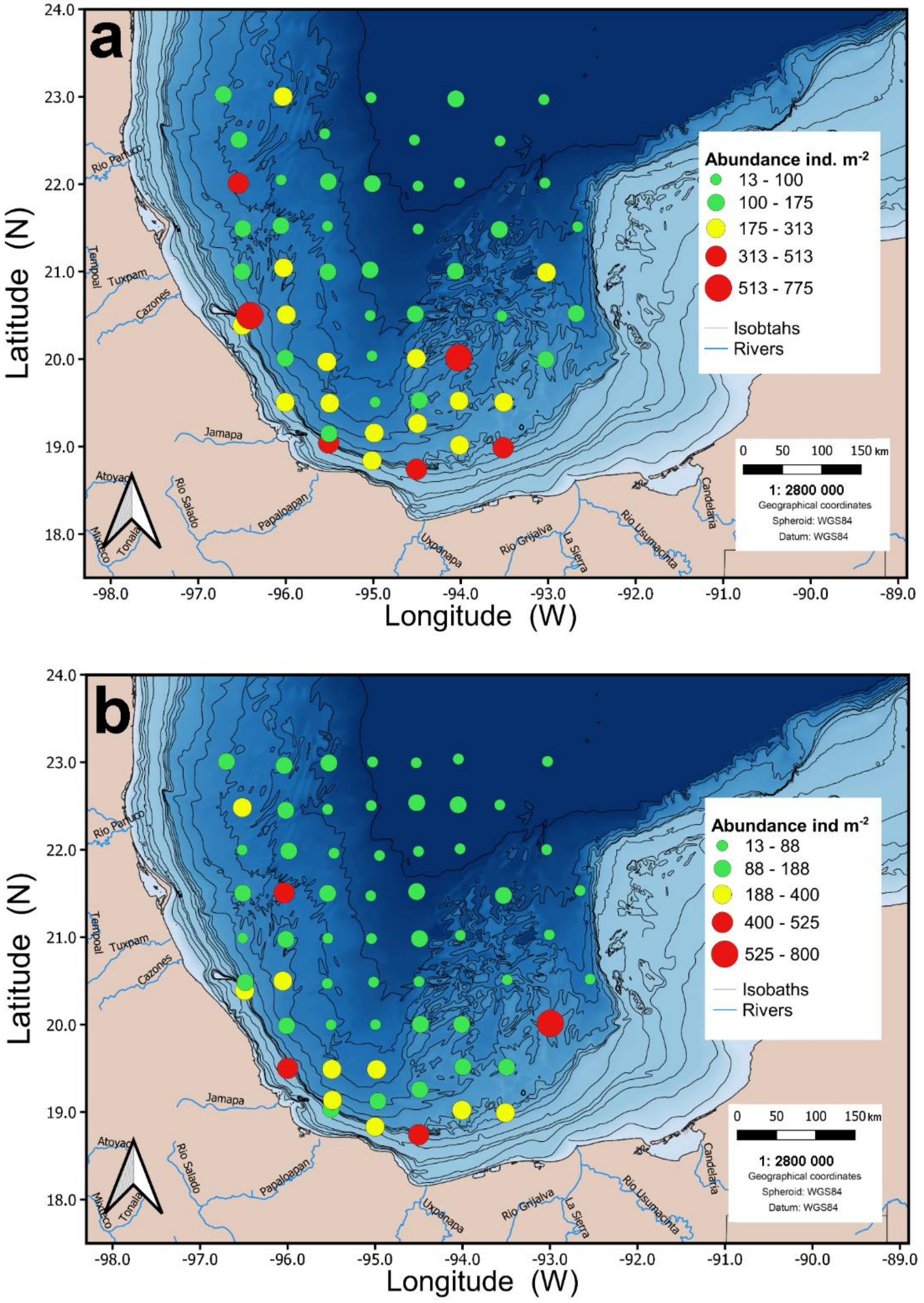


Figure 15 a-b. Spatial distribution of the polychaete abundance **a)** during SOGOM 3, **b)** during SOGOM 4.

3.2.3 Seasonal multivariate analysis

The SOGOM 3 analysis showed an overlapping of the sites of the three DC with a partial concentration of LBZ sites in the upper region of the ordination while, UBZ sites mainly grouped in the lower left region and the abyssal sites in the lower central region of the ordination (Supplementary data). The SOGOM 4 nMDS analysis showed a general less clear depth-related pattern than SOGOM 3. UBZ sites clustered on the left side and AZ sites on the right side while LBZ sites were distributed along the ordination (Supplementary data). The global R ANOSIM was 0.114 ($p = 0.003$) and 0.129 ($p = 0.003$) during SOGOM 3, and SOGOM 4, respectively. The comparison between pairs showed the following values: in SOGOM 3: 0.116 between UBZ and LBZ, 0.009 between LBZ and AZand 0.292 between AZ and UBZ ($p = 0.02$, 0.39, and 0.001, respectively) with 20, 386 and 0 permuted statistics greater than or equal to Global R, respectively. In SOGOM 4 were 0.092 between UZ and LBZ; 0.098 between LBZ and AZ, and 0.215 UBZ and AZ ($p = 0.06$, 0.026, and 0.001, respectively) with 59, 25 and 0 permuted statistics greater than or equal to Global R, respectively.

In general, the bathymetric variations of the polychaete community structure and composition were most evident during SOGOM 3 than in SOGOM 4. In both cruises the spionids presented higher relative abundances in shallow sites (up to 1300 m) and their presence and abundance decreased with increasing depth. Also, during SOGOM 3 amphinomids and glycerids were better represented at depths between 700 and 3000 m, and between 1400 and 2800 m, respectively. Lumbrinerids recorded high relative abundances in a deeper depth range (1800-3500 m). Pilargids registered low relative abundance in some shallow sites, and they presented relatively high relative abundance deeper than 2500 m (Supplementary data). During SOGOM 4 Longosomatidae presented high relative abundance at site 9 (810 m) and they were well represented in the 2000-3500 m depth range. The pylargids only presented important relative abundances in three sites at depths higher than 2700 m (17, 63 and 62) without a clear pattern (Supplementary data).

The SOGOM 3 heatmap showed that Spionidae recorded high abundance in UBZ and decreased with increasing depth, while Cirratulidae and Paraonidae recorded high abundance in LBZ and Capitellidae in AZ. The families Amphinomidae, Syllidae, Ampharetidae and Maldanidae presented the same pattern as Spionidae, more abundant in UBZ and less abundant in LBZ and AZ. Besides, Lumbrineridae, Opheliidae, Glyceridae, Orbiniidae and Phyllodocidae showed the highest abundance in LBZ. Pilargidae, Nereididae and Longosomatidae recorded their highest abundances in AZ.

In SOGOM 4 the four most abundant families were the same as in SOGOM 3, but they all recorded the highest abundance in UBZ and progressively decreased in the two deepest DC. This pattern was also found in Syllidae, Ampharetidae, Orbiniidae, Sabellidae, Maldanidae, Nephtyidae, Paralacydoniidae, Onuphidae, Cossuridae and Pilargidae. Besides, Fauveliopsidae, Glyceridae, Amphinomidae, Opheliidae, Phyllodocidae and Lumbrineridae were more abundant in LBZ than in the other two DC. In SOGOM 4 only Longosomatidae and Nereididae were more abundant in AZ (Supplementary data).

The polychaete community drivers indicated by BIOENV analyses (up to 3 factors) during SOGOM 3 were: latitude, longitude and aromatic hydrocarbons (0.14, p = 0.002), while during SOGOM 4 were: latitude, longitude and aliphatic hydrocarbons (0.25, p = 0.001) (Supplementary data).

3.2.4 Seasonal analysis of diversity estimators

The diversity bathymetric analysis revealed LBZ as the most diverse region compared with UBZ and AZ in both cruises. (Supplementary data). The highest diversity values in SOGOM 3 were recorded in the southern and northwestern regions of the study area. Also, intermediate values were registered in the same areas with some sites in the Coatzacoalcos and Campeche Canyons, the Campeche Bay salt domes zone and a site in the abyssal region. Low diversity values were recorded in practically the entire study area (Fig. 16 a). In SOGOM 4, sites of high diversity values were found in the abyssal, northwestern, and abyssal regions of the study area. Intermediate values were clearly restricted to the South and Northwest regions with two sites in the salt dome zone of the Campeche Bay and the abyssal region. As in SOGOM 3, low diversity values were recorded throughout the study area (Fig. 16 b).

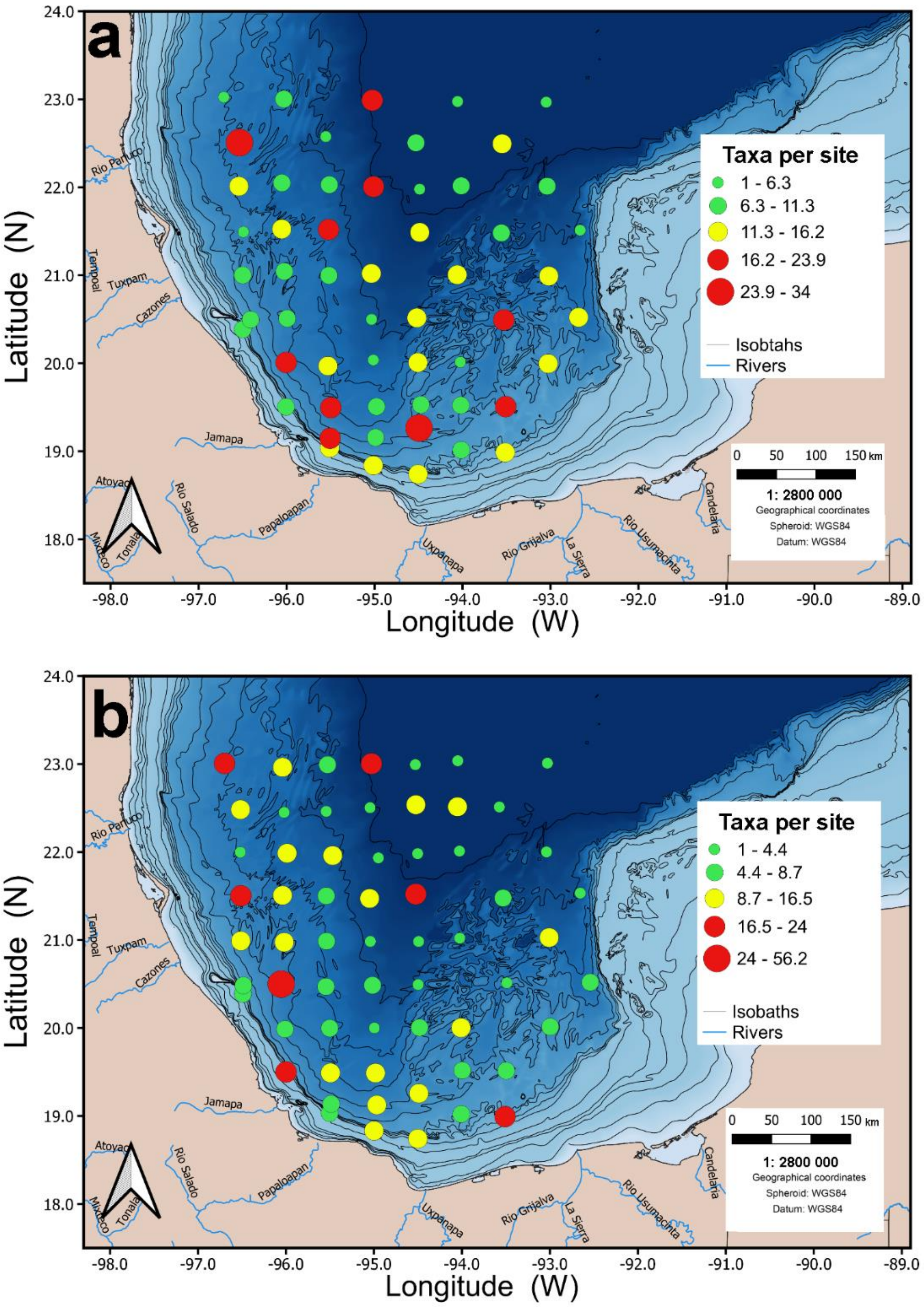


Figure 16 a-b. Spatial distribution of the polychaete diversity values **a)** during SOGOM 3, **b)** during SOGOM 4.

5. Discussion

5.1 Environmental analysis

The environmental analysis revealed a bathymetric zonation in the study area. The strong stability, observed in LBZ and AZ, stands out in the three variables measured in the bottom water (salinity, temperature, and dissolved oxygen). In UBZ these factors showed important variations. Analysis of environmental factors allowed us to characterize the UBZ as a region with highest values of temperature, silt, organic matter, and aromatic hydrocarbons besides the LBZ showed intermediate values of carbonate, silt clay, organic matter, and PAHs meanwhile the AZ was characterized by high carbonate, clay, and low silt, organic matter, and PAHs concentration. A most detailed discussion of the results obtained in the environmental analysis can be consulted in Quintanar-Retama et al., (2022, 2023).

In the seasonal analysis, the OM ($p = 0.57$) and carbonate content ($p = 0.89$) did not show significant difference between SOGOM 3, and SOGOM 4. The most important variations in abiotic factors during seasonal analysis was observed in the sediment granulometry. During SOGOM 3 the lower silt and clay values were registered from 185 to 1000 m and from 1000 to 3750 m depth ranges, respectively. While, in SOGOM 4 we registered the highest values for both factors in these depth ranges, also, respectively. Variations in the sediment granulometry have been reported as a seasonal consequence (Selvaraj et al., 2015) that could mean variations in the continental sediments input to the region and has been related with variations in the fauna community structure (Etter and Grassle, 1992).

5.2 Faunal analysis

The most abundant families recorded in this study are typical deep sea taxa. Spionids, paraonids, cirratulids and capitellids have been recorded as abundant and widely distributed taxa in the deep sea from other regions (Cosson-Sarradin et al., 1998; Glover et al., 2001; Paterson et al., 1998), in north of the GoM (Carvalho et al., 2013; Reuscher and Shirley, 2017) and from the study area (Pérez-Mendoza et al., 2003; Quintanar-Retama et al., 2022). In the seasonal analysis, the taxonomic composition was very similar between cruises. Thirty-six families were recorded in both samplings and only four were exclusive to SOGOM 3 (Hesionidae, Lacydoniidae, Pectinariidae and Serpulidae) and another four to SOGOM 4 (Magelonidae, Sabellariidae, Sphaerodoridae and Uncispionidae). Polychaete communities were dominated by the same families on both cruises. Nine of the ten most abundant families were the same in both cruises, together with Syllidae in SOGOM 3 and Longosomatidae in SOGOM 4. The ten dominant taxa represented 73% of abundance during SOGOM 3 and 72% during SOGOM 4 and recorded a very similar relative abundance between samplings.

Abundance decreased with increasing depth. This pattern was widely documented in the deep sea (Baldrighi et al., 2014; Bernardino et al., 2016; Gage and Tyler, 1991; Hessler and Sanders, 1967) and was suggested to be related to the decrease of organic matter availability with depth (Morse and Beazley, 2008) and with distance to the coast (Escobar-Briones and García-Villalobos, 2009; Morse and Beazley, 2008; Wei et al., 2010). We observed the same trend in OM content in sediments, decreasing with increasing depth in the four samplings analyzed.

However, this pattern presented some variations in several sites mainly located in the region of the Campeche Bay salt domes zone where the presence of a cyclonic gyre has been reported (Díaz-Flores et al., 2017) and also a couple at the continental rise is found. Cyclonic gyres raise the pycnocline itowards the photic zone, carrying the nutrients upward and making them available to autotrophic communities, which can promote important phytoplankton blooms (Mcwilliams, 2008) The effect of cyclonic gyres on primary productivity increases the availability of potentially transferable organic matter to deep-sea areas. On the other hand, the continental rise region showed a higher sedimentation rate (Díaz-Asencio et al., 2019) which favors the accumulation of organic matter and can support high abundance.

The average abundance recorded in this study (120 ind. m^{-2}, in a range from 9 to 583 ind. m^{-2}) are lower than those recorded in other studies (Carvalho et al., 2013; Qu et al., 2017, 2016; Reuscher and Shirley, 2017). However, direct comparisons require considering the type of device used to sample, the sampling depth and the sieve mesh size used. In this sense, our relatively low abundance values are largely explained by using a mesh size of 500 microns.

In the seasonal analysis, we did not register significant differences in abundance between cruises or when comparing each depth category of SOGOM 3 with its respective one of SOGOM 4. In this region, significant differences in abundance of the macrofauna have been recorded between samplings carried out in different seasons (Quintanar-Retama et al., 2023). Thus, seasonal changes in the macrofauna abundance in this region would be related to taxonomic groups other than polychaetes.

In SOGOM 3, the sites that differ from the general abundance depth-related pattern were 7, 24 and 32 located within the Coatzacoalcos Canyon. The central zone of a canyon usually presents a higher sedimentation rate and therefore OM accumulation (Escobar-Briones et al., 2008), which could explain these results. Furthermore, during SOGOM 4, site 18 also recorded higher abundance than adjacent sites in the depth profile. This site was located in a region where a cyclonic gyre has been reported (Díaz-Flores et al., 2017), which implies greater productivity and consequent export of organic matter to the deep sea and could explain our results.

The spatial distribution of the abundance values partially agree with what was previously reported in the study area (Quintanar-Retama et al., 2023, 2022). High and intermediate values were recorded at sites in the southern region near the coastline, in front of the Tecolutla River mouth, and in the salt dome zone of the Campeche Bay. The proximity to the coastline could explain the reason of the high abundances in the southern region and in the Tecolutla mouth River, due to the OM input from the continent. In the Campeche Bay salt domes zone, we recorded intermediate abundance values in SOGOM 3 and intermediate and high values during SOGOM 4. The presence of chemoautotrophic communities that tend to increase the regional abundance, the organic matter input due to the Campeche gyre and the discharges of the Grijalva Usumacinta river system could explain these results. We also observed two sites with intermediate values at the continental rise, an area with a high sedimentation rate (Díaz-Asencio et al., 2019). All sites in the northern region recorded low abundance values. These sites are deeper and farther from the coastline, which decreases the organic matter availability (Escobar-Briones and García-Villalobos, 2009). The spatial distribution of the abundance values in the temporal analysis was very similar to that observed during the regional analysis. Comparatively, during SOGOM 3 the sites with intermediate values reach latitudes slightly further north than during SOGOM 4.

5.3 Multivariate analysis

Detected variations in the polychaete community structure related to depth in this study were widely documented in deep sea (Bernardino et al., 2016; Levin et al., 2001; Woolley et al., 2016). The community structure of the contiguous DC was more similar than the depth profile extremes (UBZ and AZ). The main structure community variations were due to the better spionids representation in UBZ; glycerids and amphinomids at intermediate depths (LBZ) and pylargids and longosomatids in AZ. Besdies, Sabellaridae, Sigalionidae, Sphaerodoridae and Uncispionidae were only recorded in UBZ, while Chaetopteridae, Pectindariidae, Serpulidae and Sigalionidae were recorded merely in LBZ. Oenonidae in LBZ and AZ and Travisiidae only in AZ.

In the temporal analysis, despite a less clear pattern, in SOGOM 3 we confirmed the results observed in the regional study. The main bathymetric community variations were due again to the better spionids representation in UBZ; glycerids and amphinomids in LBZ and pilpargids and ophelids in the sites of the abyssal region. In SOGOM 4 the pattern of the polychaete community was even less clear. The main bathymetric community changes were due again to the better spionids representation in UBZ; glycerids and amphinomids in LBZ and pilpargids and ophelids in the sites of the abyssal region.

The most correlated environmental factors with faunal distribution were (up to three factors) OM, DO and latitude. The first two have been recorded as important deep sea benthic communities drivers (Bernardino et al., 2016; Cosson et al., 1997; Levin and Sibuet, 2012). Latitude has also been related to variations in the composition of the benthic macrofauna community (Gage, 2004; Poore and Wilson, 1993; Rex et al., 2005), but in this sudy was strong correlated with depth, OM and carbonate. In the seasonal analysis, the BIOENV showed a very low correlation between the biotic and abiotic similarity matrices in both cruises. This is partly due to the unclear pattern recorded in the community distribution through the depth gradient.

5.4 Diversity estimators

The diversity bathymetric pattern recorded in the regional analysis was the typical deep sea one. The highest diversity values were registered in intermediate depths (LBZ) and the lowest ones in UBZ and AZ (Etter and Grassle, 1992; Ramirez-Llodra et al., 2010; Rex, 1981; Rex et al., 2006). This pattern was also recorded in both cruises during the seasonal analysis. The diversity spatial distribution showed the highest values in the southern regions, in the Campeche Bay salt domes zone, in the Campeche Canyon and in the northeast of the study area. These sites corresponded to the LBZ, which could explain these results, since it is the bathymetric region that typically registers the greatest diversity in the deep sea. Some authors maintain that this is due to the physiological bottleneck generated by hydrostatic pressure and temperature that promote faunal zonation, preventing the wide shallower water taxa distribution (Brown and Thatje, 2014). They place this neck in LBZ and maintain that they promote speciation in that region. Some sites in the abyssal region also recorded relatively high diversity values. The abyssal plain has been documented as a region with low abundance values but where important diversity values are usually recorded (Ramirez-Llodra et al., 2010; Sanders, 1968). In the seasonal analysis, we observed both on SOGOM 3 and at SOGOM 4 the northeastern was registered as high diversity region. Whereas, the south region registered high diversity values during SOGOM 3 and intermediate in SOGOM 4 probably due to the abundance difference registered between cruises.

6. Conclusions

This study contributes to the understanding of polychaete communities in deep Mexican waters of the Gulf of Mexico. The environmental analysis showed the bathymetric gradient effect in the study area. The abyssal region sites were characterized by high carbonate, clay and dissolved oxygen concentrations, while the highest values of temperature, silt, organic matter and aromatic hydrocarbons were recorded in UBZ. We collected 1968 specimens belonging to 45 polychaete families. The ten most abundant families were: Spionidae, Paraonidae, Capitellidae, Cirratulidae, Amphinomidae, Opheliidae, Pilargidae, Lumbrineridae, Longosomatidae and Glyceridae. Together they represented 70% of the overall abundance. The families with the most records were Cirratulidae, Capitellidae, Paraonidae, Spionidae and Opheliidae present in at least 41 sampling sites. The highest abundance values were recorded in shallow sites in the southern region and close to the coastline. On the other hand, the lowest values were registered in the northern region sites particularly, in the abyssal zone. Intermediate abundance values were recorded in the Campeche Bay salt domes zone and in the Coatzacoalcos and Campeche Canyons. The main polychaete community drivers were latitude, bottom water dissolved oxygen and sediment organic matter content. We observed depth-related variations in the community structure. The greatest taxonomic diversity was recorded at intermediate depth sites in the southern and northwestern regions and in the Campeche Bay salt domes zone, as well as some sites in the abyssal region. The temporal analysis highlighted variations in sediment composition between cruises and higher abundance during SOGOM 3 compared to SOGOM 4 that may be related to seasonal fluctuations. The taxonomic composition was very similar between cruises. Thirty-six families were registered in both samplings and only four were exclusive to each of them. We recorded the same dominant families in both samplings. Nine of the ten most abundant families were the same in both cruises. The results of this study constitute an important contribution to the general understanding of the Gulf of Mexico and a baseline for further ecological studies of infaunal communities in the region.

7. Acknowledgments

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Supplementary material

Abundance matrix

https://docs.google.com/spreadsheets/d/1Ze0pkwo7e2_FVOyrFE6zViZL9IVkn9ac/edit?usp=share_link&ouid=108144172576868121260&rtpof=true&sd=true

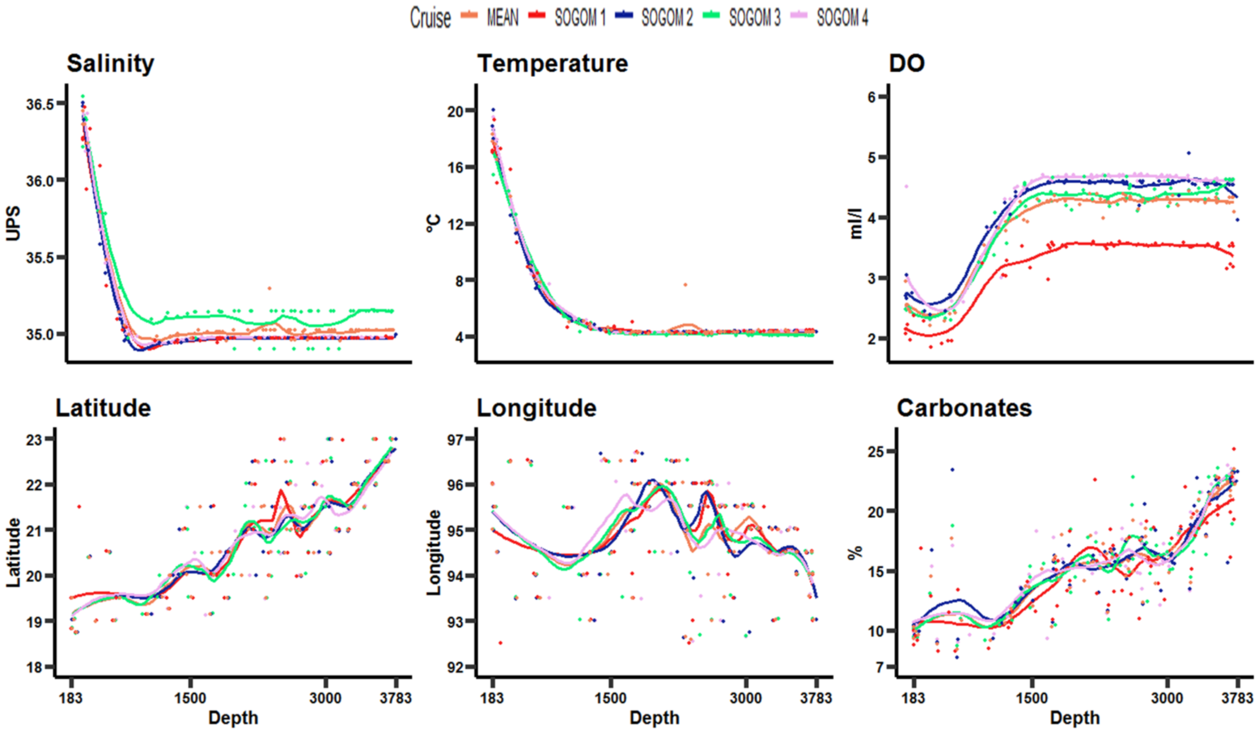


Figure 1. Depth related pattern of environmental factors. DO = Dissolved oxygen.

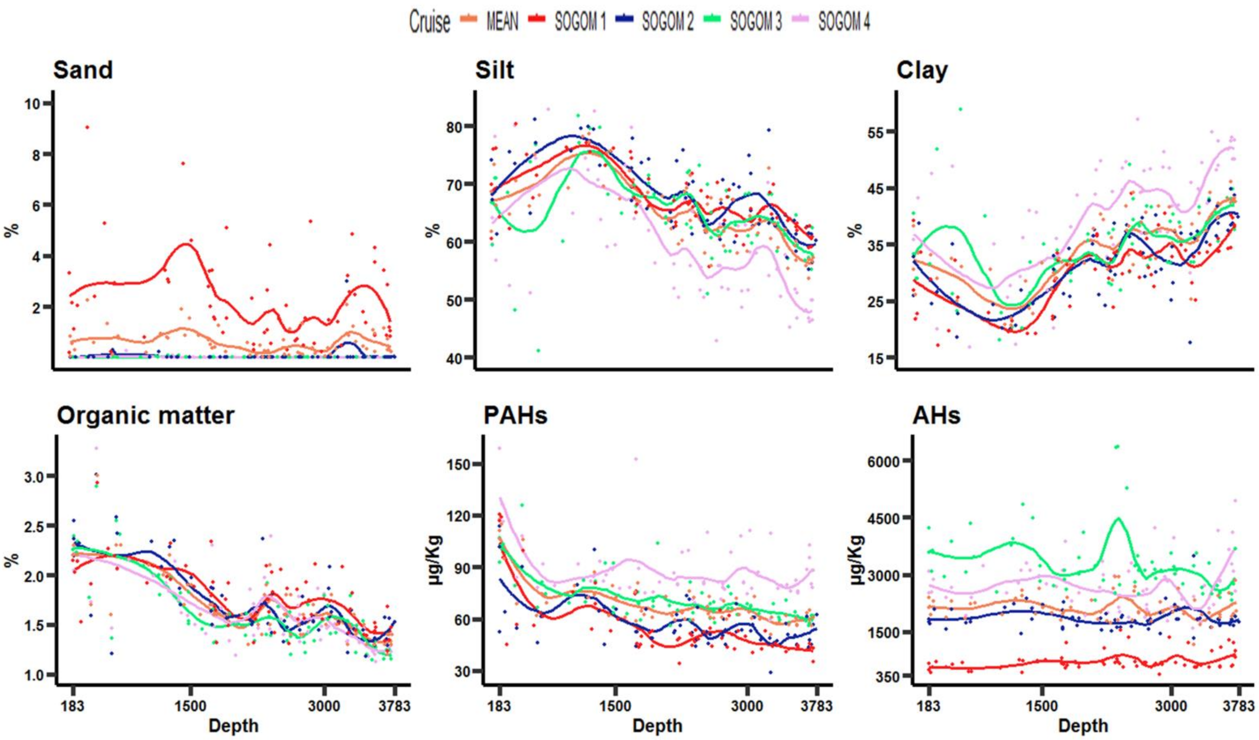


Figure 2. Depth related pattern of environmental factors. AHs = Aliphatic hydrocarbons, PAHs = Polycyclic Aromatic Hydrocarbons.

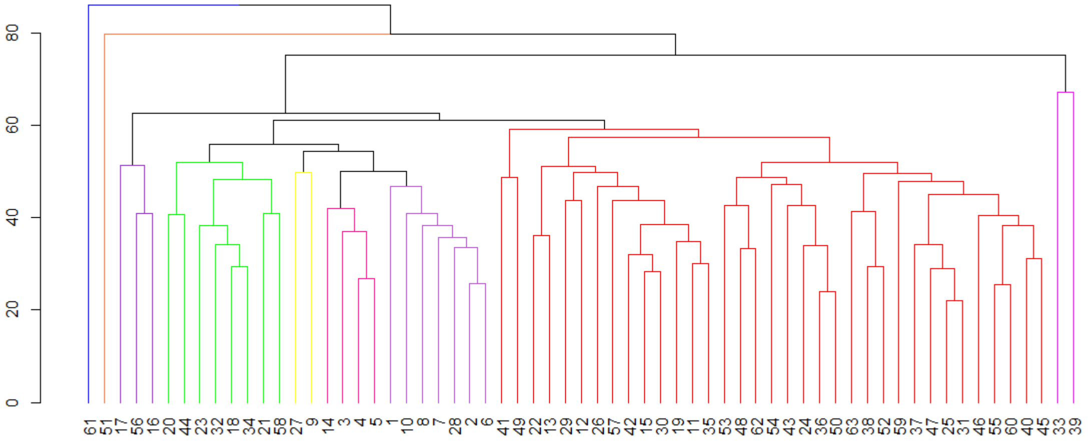


Figure 3. Cluster of polychaete communities during SOGOM 1-4 (group average mode) with SIMPROF test based on Bray Curtis similarities.

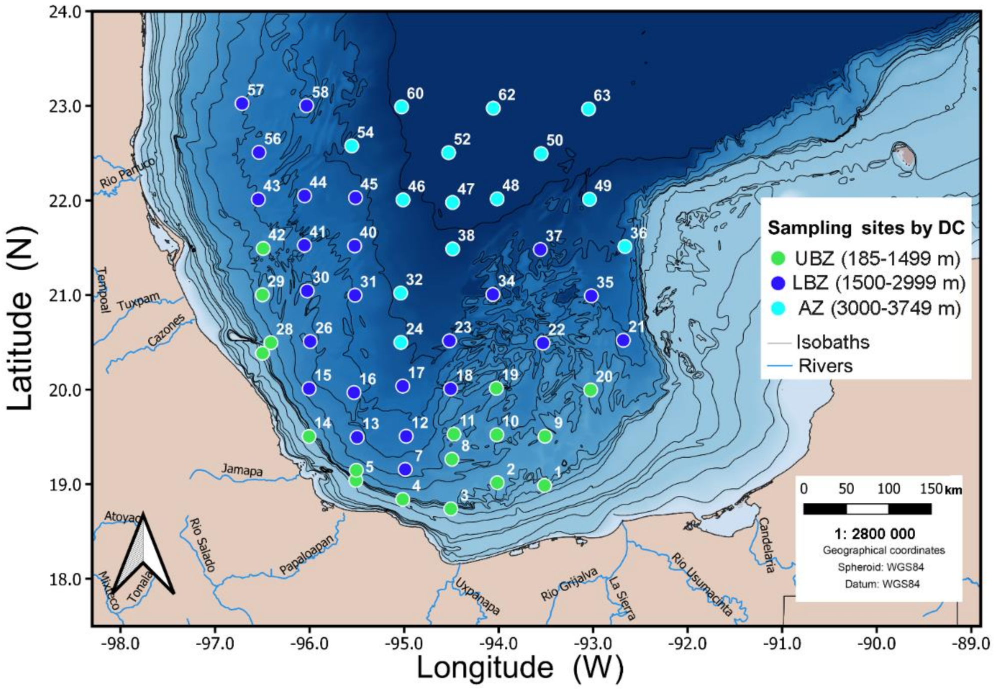


Figure 4. Location of the 55 sampling sites during the oceanographic cruise SOGOM 3. Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

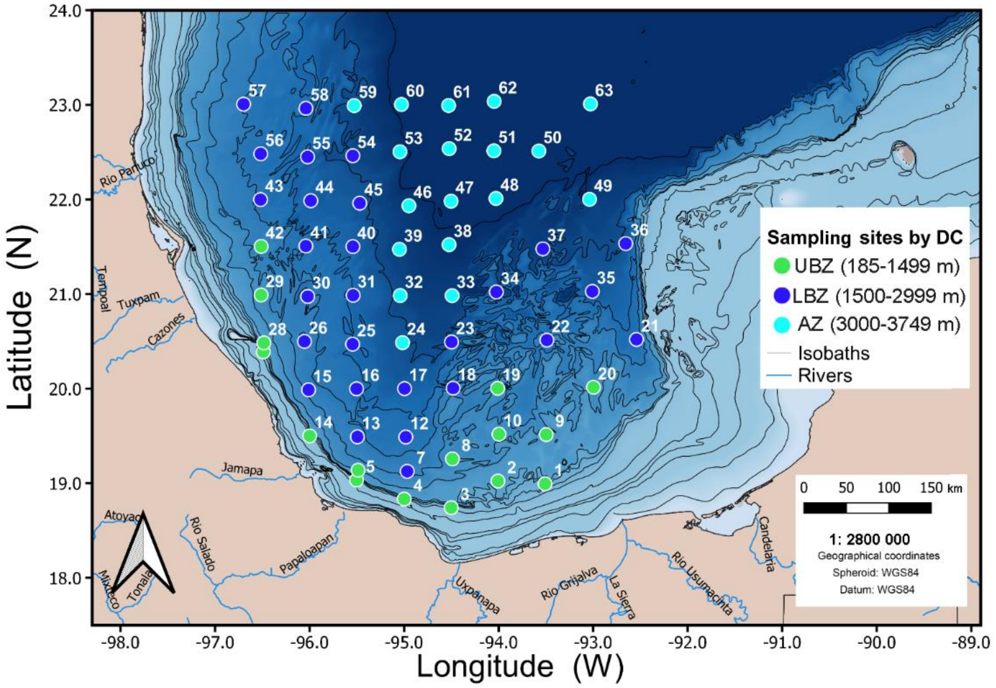


Figure 5. Location of the 62 sampling sites during the oceanographic cruise SOGOM 4. Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

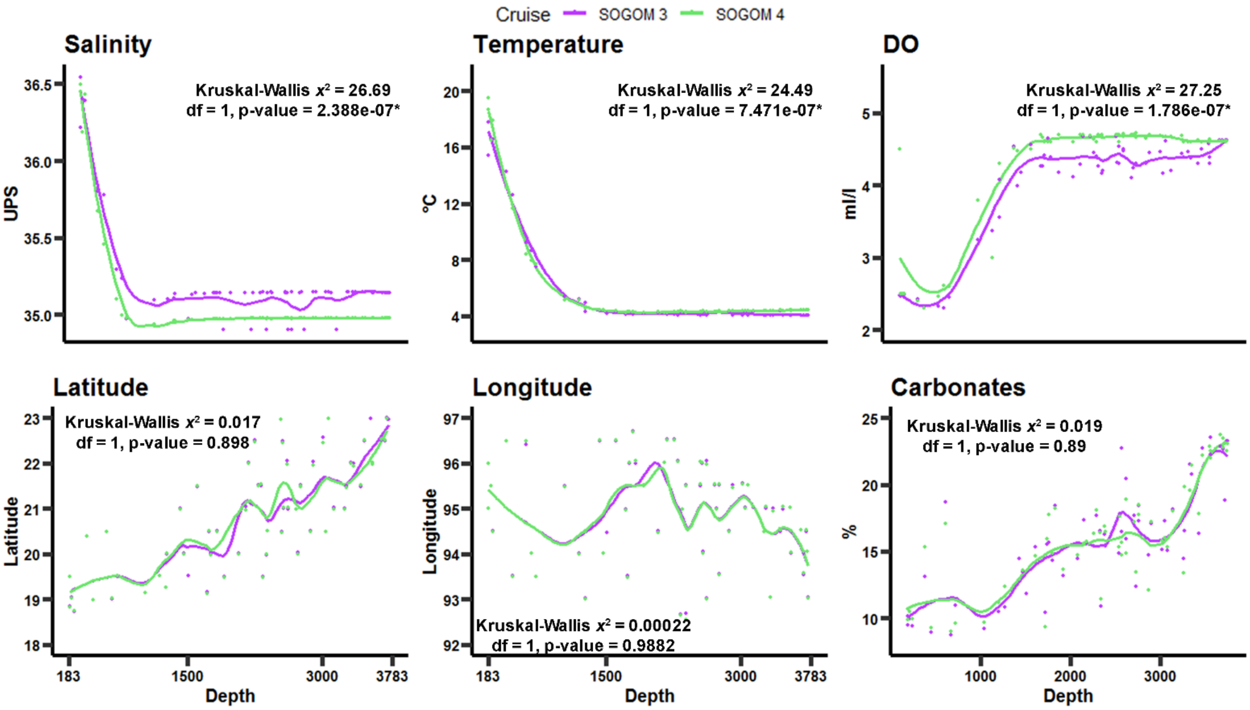


Figure 6. Depth related pattern of environmental factors. DO = Dissolved oxygen. * = significant difference.

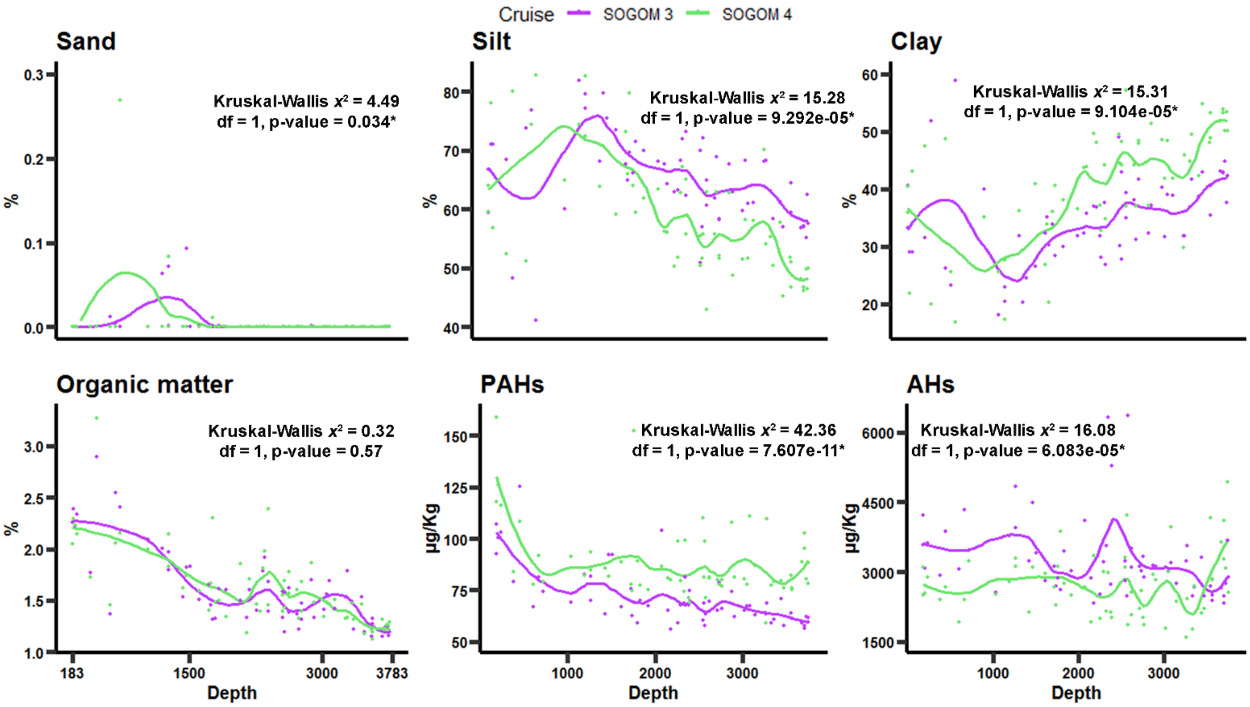


Figure 7. Depth related pattern of environmental factors. AHs = Aliphatic hydrocarbons, PAHs = Polycyclic Aromatic Hydrocarbons. * = significant difference.

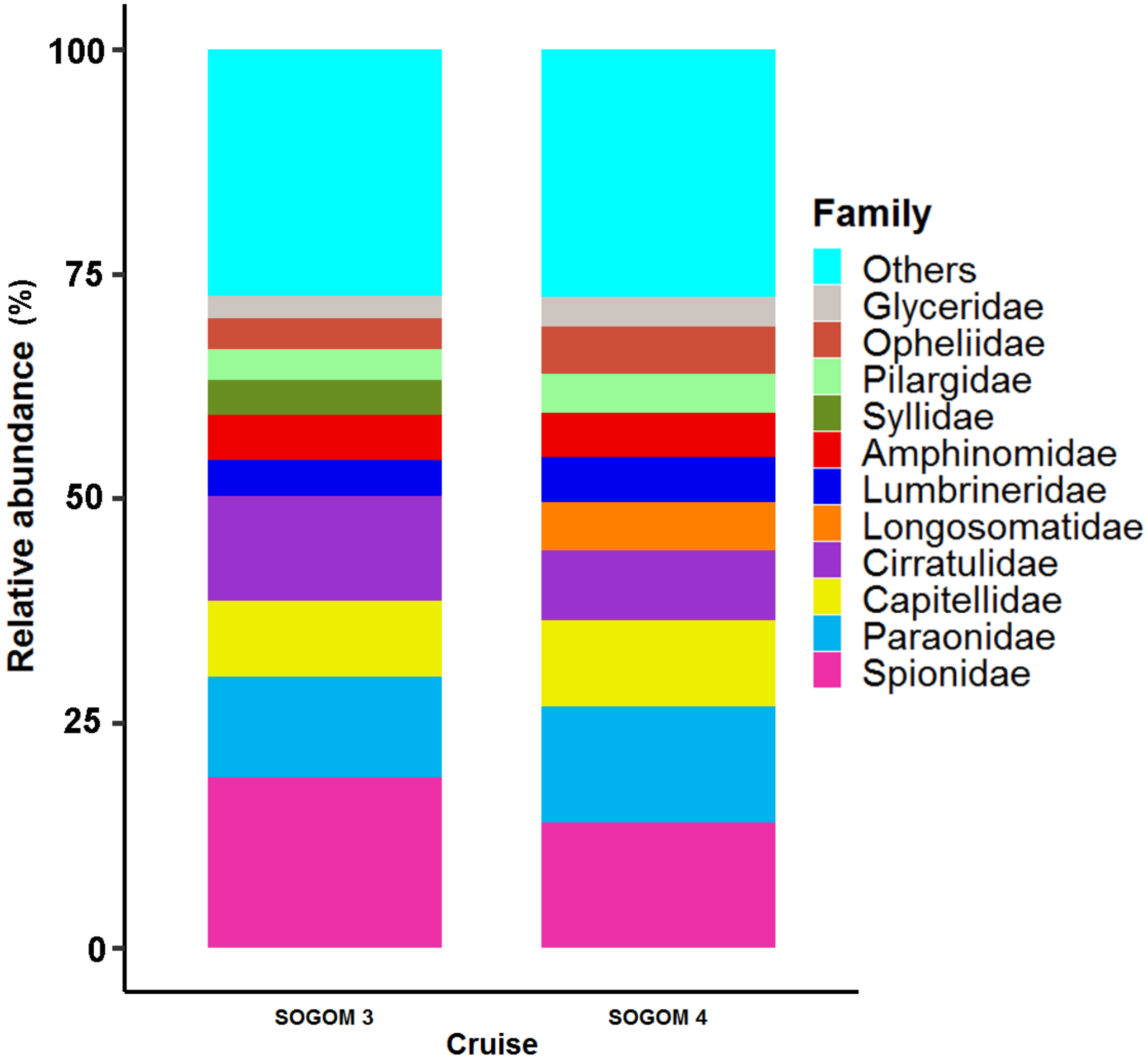


Figure 8. Ten most abundant polychaete families during SOGOM 3 and SOGOM 4.

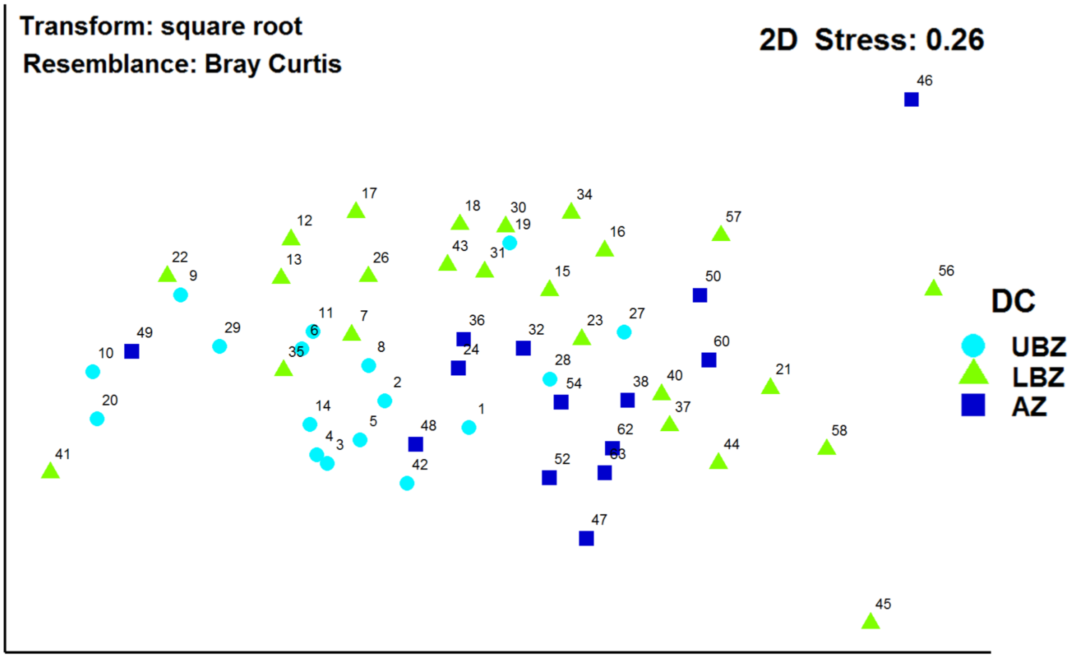
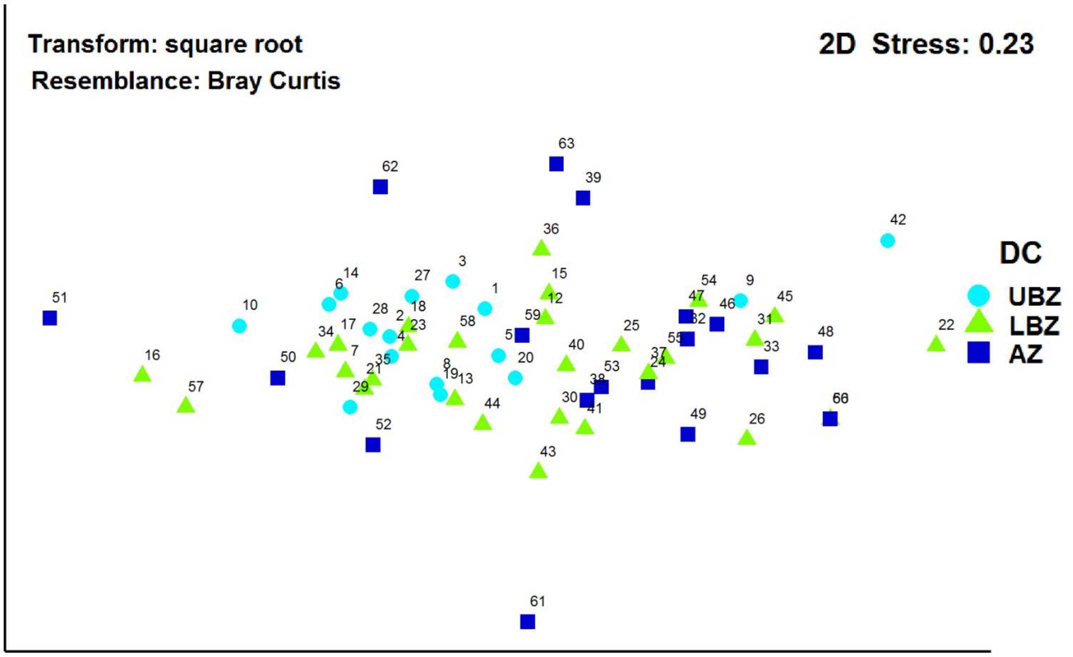


Figure 9. SOGOM 3 Polychaete non-metric multidimensional scaling based on Bray Curtis similarities. Upper bathyal zone (UBZ- blue circle), lower bathyal zone (LBZ-green triangles), and abyssal zone (AZ-blue square).



Figures 10. Non-metric multidimensional scaling of polychaete communities during SOGOM 4 based on Bray Curtis similarities. Upper bathyal zone (UBZ- blue circle), lower bathyal zone (LBZ-green triangles), and abyssal zone (AZ-blue square).

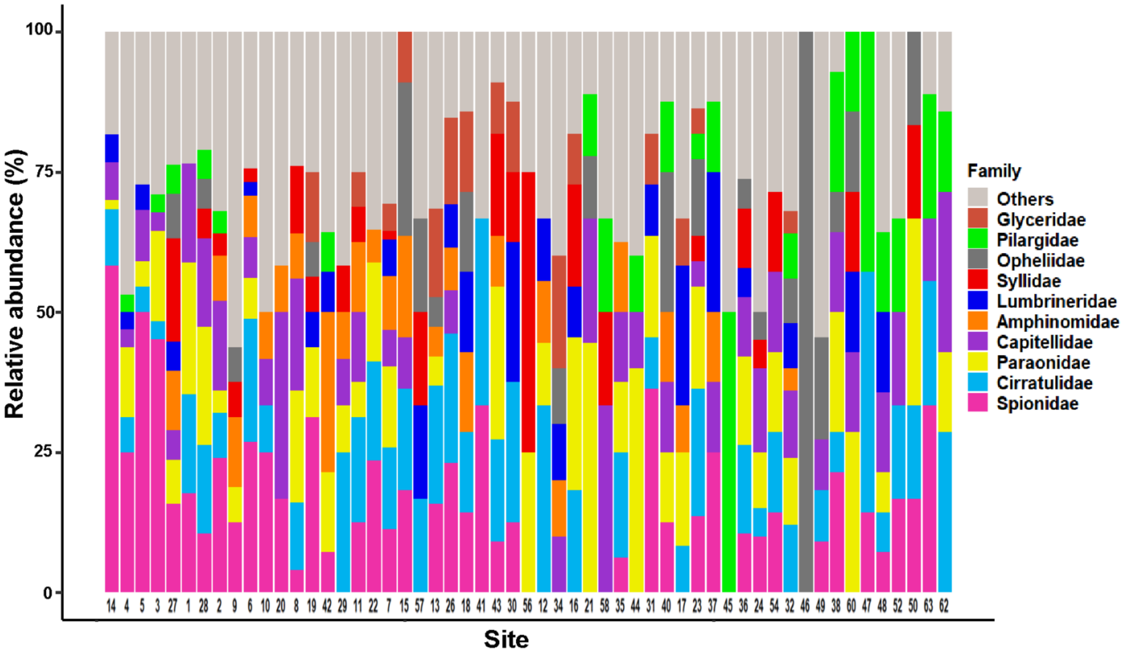


Figure 11. Relative abundance of polychaete families related to depth during SOGOM 3. Sites were ordered from left to right from shallowest to deepest.

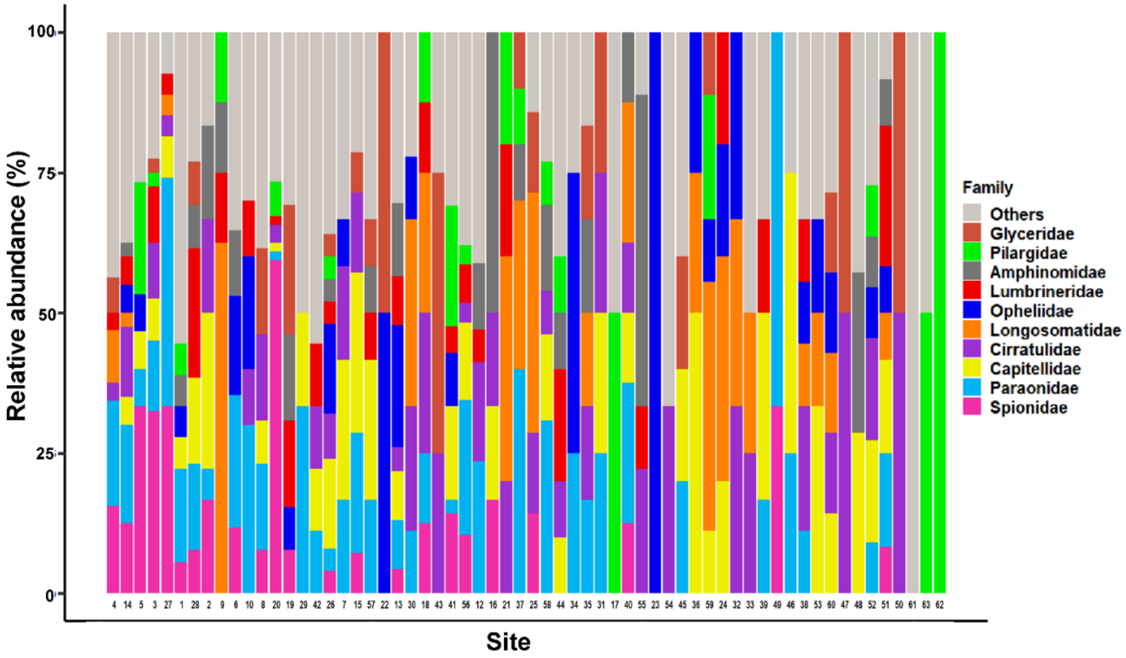
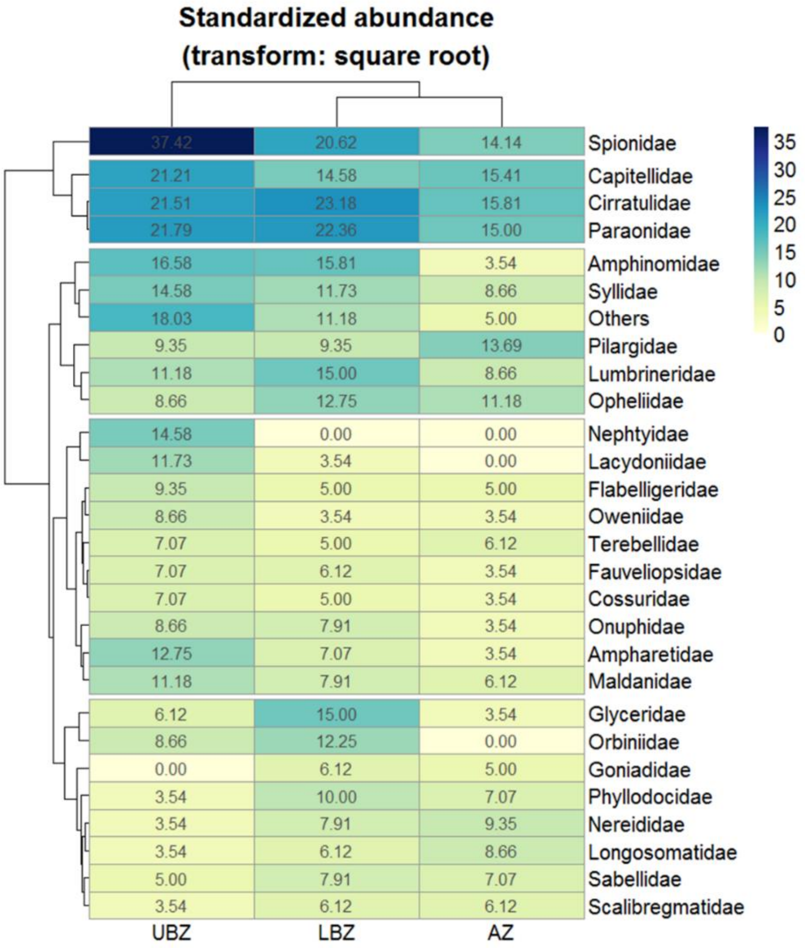
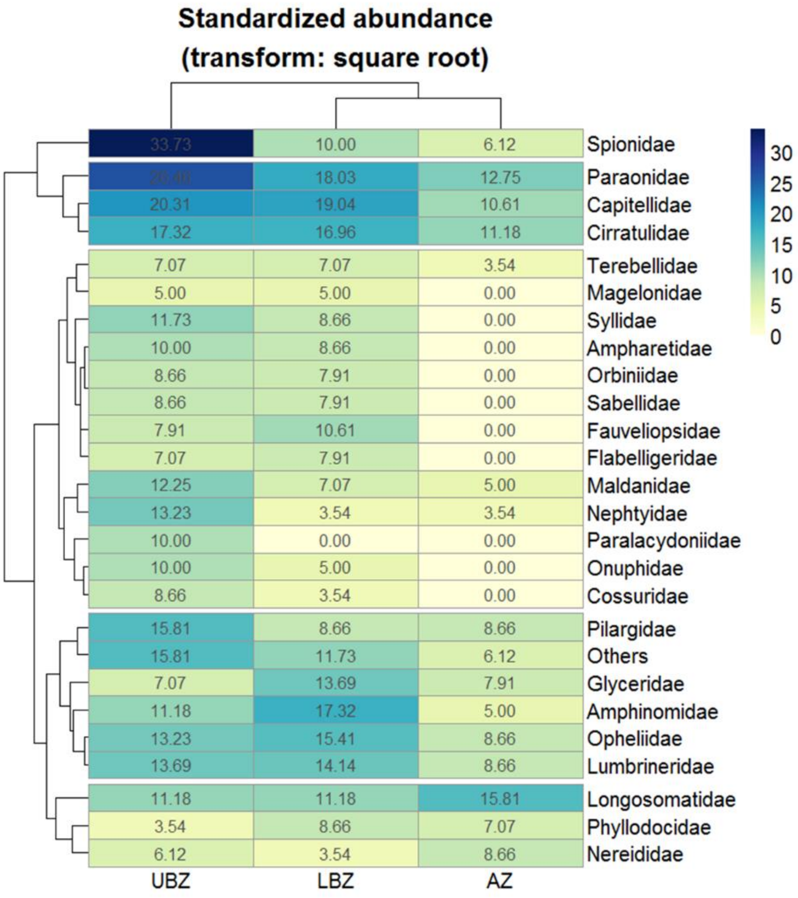


Figure 12. Relative abundance of polychaete families related to depth during SOGOM 4. Sites were ordered from left to right from shallowest to deepest.



	UBZ	LBZ	AZ
Spionidae	37.42	20.62	14.14
Capitellidae	21.21	14.58	15.41
Cirratulidae	21.51	23.18	15.81
Paraonidae	21.79	22.36	15.00
Amphinomidae	16.58	15.81	3.54
Syllidae	14.58	11.73	8.66
Others	18.03	11.18	5.00
Pilargidae	9.35	9.35	13.69
Lumbrineridae	11.18	15.00	8.66
Opheliidae	8.66	12.75	11.18
Nephtyidae	14.58	0.00	0.00
Lacydoniidae	11.73	3.54	0.00
Flabelligeridae	9.35	5.00	5.00
Oweniidae	8.66	3.54	3.54
Terebellidae	7.07	5.00	6.12
Fauveliopsidae	7.07	6.12	3.54
Cossuridae	7.07	5.00	3.54
Onuphidae	8.66	7.91	3.54
Ampharetidae	12.75	7.07	3.54
Maldanidae	11.18	7.91	6.12
Glyceridae	6.12	15.00	3.54
Orbiniidae	8.66	12.25	0.00
Goniadidae	0.00	6.12	5.00
Phyllodocidae	3.54	10.00	7.07
Nereididae	3.54	7.91	9.35
Longosomatidae	3.54	6.12	8.66
Sabellidae	5.00	7.91	7.07
Scalibregmatidae	3.54	6.12	6.12

Figure 13. Heatmap of the abundance of polychaete families during SOGOM 3. Upper bathyal zone (UBZ), lower bathyal zone (LBZ), and abyssal zone (AZ).



	UBZ	LBZ	AZ
Spionidae	33.73	10.00	6.12
Paraonidae	26.46	18.03	12.75
Capitellidae	20.31	19.04	10.61
Cirratulidae	17.32	16.96	11.18
Terebellidae	7.07	7.07	3.54
Magelonidae	5.00	5.00	0.00
Syllidae	11.73	8.66	0.00
Ampharetidae	10.00	8.66	0.00
Orbiniidae	8.66	7.91	0.00
Sabellidae	8.66	7.91	0.00
Fauveliopsidae	7.91	10.61	0.00
Flabelligeridae	7.07	7.91	0.00
Maldanidae	12.25	7.07	5.00
Nephtyidae	13.23	3.54	3.54
Paralacydoniidae	10.00	0.00	0.00
Onuphidae	10.00	5.00	0.00
Cossuridae	8.66	3.54	0.00
Pilargidae	15.81	8.66	8.66
Others	15.81	11.73	6.12
Glyceridae	7.07	13.69	7.91
Amphinomidae	11.18	17.32	5.00
Opheliidae	13.23	15.41	8.66
Lumbrineridae	13.69	14.14	8.66
Longosomatidae	11.18	11.18	15.81
Phyllodocidae	3.54	8.66	7.07
Nereididae	6.12	3.54	8.66

Figure 14. Heatmap of the abundance of polychaete families during SOGOM 4. Upper bathyal zone (UBZ), lower bathyal zone (LBZ), and abyssal zone (AZ).

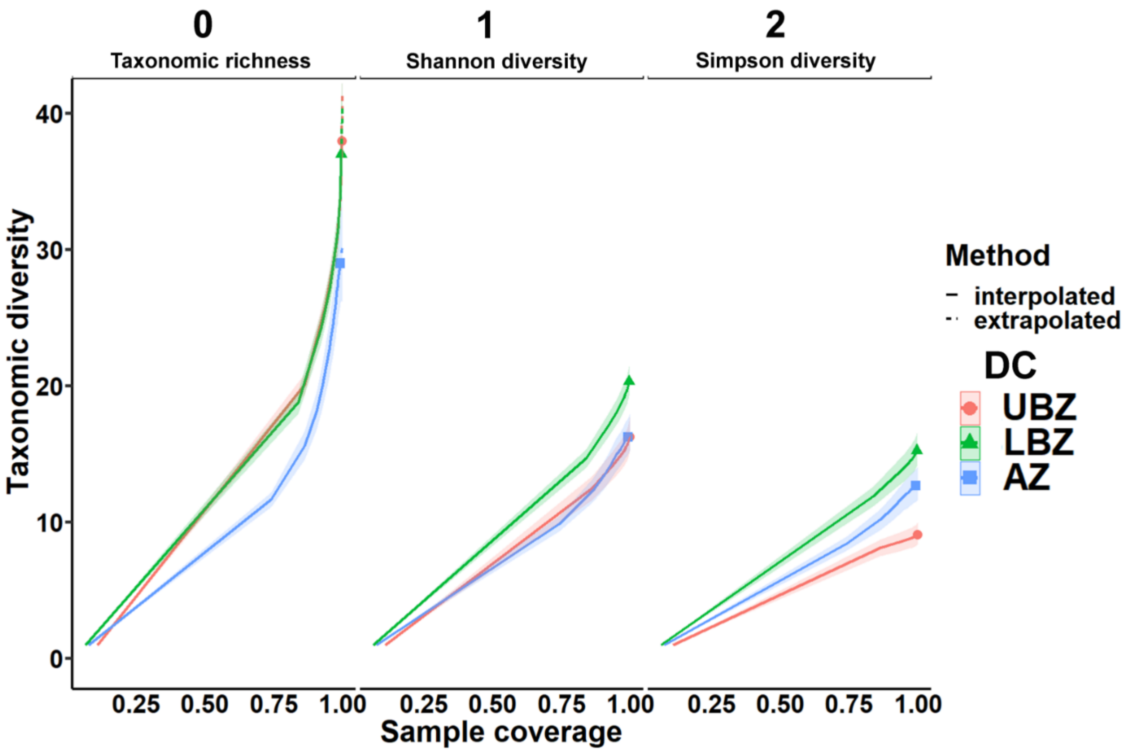


Figure 15. SOGOM 3 coverage-based R/E (rarefaction and extrapolation) sampling curves for three Hill numbers (q = 0, 1, and 2). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

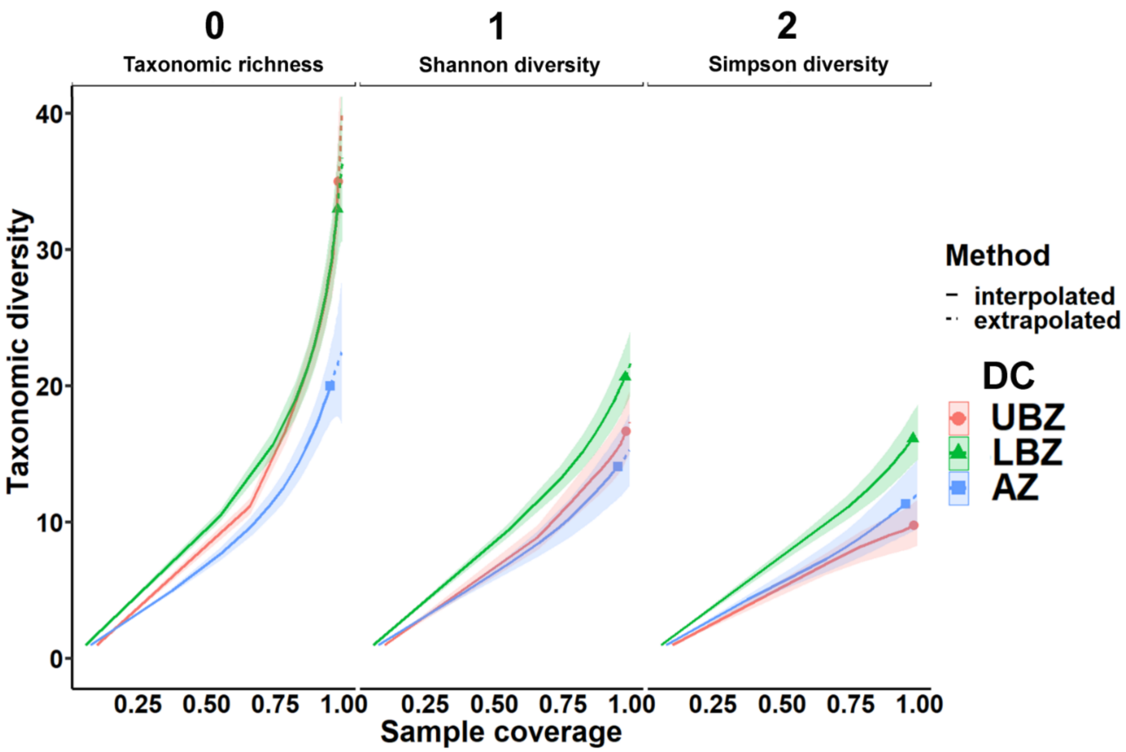


Figure 16. SOGOM 4 coverage-based R/E (rarefaction and extrapolation) sampling curves for three Hill numbers (q = 0, 1, and 2). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

Table 1

Families taxonomic list of the Southern Gulf of Mexico depth waters

---

- Phylum Annelida Lamarck, 1802
  - Class Polychaeta Grube, 1850
    - Subclass Polychaeta incertae sedis
      - Family Oweniidae Rioja, 1917
    - Subclass Errantia Audouin & H Milne Edwards, 1832
      - Order Amphinomida
        - Family Amphinomidae Lamarck, 1818
      - Order Eunicida
        - Family Dorvilleidae Chamberlin, 1919
        - Family Lumbrineridae Schmarda, 1861
        - Family Oenonidae Kinberg, 1865
        - Family Onuphidae Kinberg, 1865
      - Order Phyllodocida Dales, 1962
        - Family Glyceridae Grube, 1850
        - Family Goniadidae Kinberg, 1866
        - Family Hesionidae Grube, 1850

- Family Lacydoniidae Bergström, 1914
- Family Nephtyidae Grube, 1850
- Family Nereididae Blainville, 1818
- Family Paralacydoniidae Pettibone, 1963
- Family Phyllodocidae Örsted, 1843
- Family Pilargidae Saint-Joseph, 1899
- Family Polynoidae Kinberg, 1856
- Family Sigalionidae Kinberg, 1856
- Family Sphaerodoridae Malmgren, 1867
- Family Syllidae Grube, 1850

Subclass Sedentaria Lamarck, 1850
- Family Chaetopteridae Audouin & Milne Edwards, 1833

Infraclass Canalipalpata Rouse & Fauchald, 1997
- Family Sabellariidae Johnston, 1865

Order Sabellida Levinsen, 1883
- Family Sabellidae Latreille, 1825
- Family Serpulidae Rafinesque, 1815

Order Spionida Rouse & Fauchald, 1997
- Family Spionidae Grube, 1850
- Family Longosomatidae Hartman, 1944
- Family Poecilochaetidae Hannerz, 1956
- Family Trochochaetidae Pettibone, 1963
- Family Uncispionidae Green, 1982

Order Terebellida Rouse & Fauchald, 1997
- Family Ampharetidae Malmgren, 1866
- Family Cirratulidae Ryckholt, 1851
- Family Fauveliopsidae Hartman, 1971
- Family Flabelligeridae de Saint-Joseph, 1894
- Family Pectinariidae Quatrefages, 1866
- Family Sternaspidae Carus, 1863
- Family Terebellidae Johnston, 1846
- Family Trichobranchidae Malmgren, 1866

Infraclass Scolecida Rouse & Fauchald, 2001
- Family Capitellidae Grube, 1862
- Family Cossuridae Day, 1963
- Family Magelonidae Cunningham & Ramage, 1888
- Family Maldanidae Malmgren, 1867
- Family Opheliidae Malmgren, 1867
- Family Orbiniidae Hartman, 1942
- Family Paraonidae Cerruti, 1909
- Family Scalibregmatidae Malmgren, 1867
- Family Travisiidae Hartmann-Schröder, 1971

Table 2.
SOGOM 1-4BIOENV
results

Factors	size	correlation
lat	1	0.3563
lat do	2	0.3504
lat do om	3	0.3435
lat long do silt	4	0.3280
lat long do om silt	5	0.3269
lat long depth do om silt	6	0.3215
lat long depth do alh om silt	7	0.3158
lat long depth do arh alh om silt	8	0.3080
lat long depth temp do arh alh om silt	9	0.2973

Table 3
SOGOM 3 BIOENV results.

Factors	size	correlation
lat	1	0.1133
lat long	2	0.1319
lat long arh	3	0.1371
lat long arh alh	4	0.1348
lat long arh alh om	5	0.1198
lat long depth arh alh om	6	0.1015
lat long depth arh alh om silt	7	0.0841
lat long depth do arh alh om silt	8	0.0676
lat long depth temp do arh alh om silt	9	0.0539

Table 4
SOGOM 3 BIOENV results.

Factors	size	correlation
lat	1	0.2067
lat long	2	0.2365
lat long alh	3	0.2464
lat long depth alh	4	0.2344
lat long depth alh silt	5	0.2177
lat long depth do alh silt	6	0.1995
lat long depth do alh om silt	7	0.1845
lat long depth temp do alh om silt	8	0.1459

lat long depth temp do arh alh om silt	9	0.1191

Title page

Title: Diversity and, abundance patterns of macrofauna Peracarida (Arthropoda, Crustacea) from deep sea southwestern Gulf of Mexico

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Abstract:

The Peracarida macrofauna collected in 63 sites of a large geographical area (92.67°–96.70°W 18.74°–23.04° N) and wide bathymetric gradient (185-3740 m depth) of the deep sea of the southwestern Gulf of Mexico was analyzed. Samples were obtained with a Reineck-type box corer on board the R/V Justo Sierra (Universidad Nacional Autónoma de México) during the oceanographic cruises SOGOM 1-4 (June 3–27, 2015; August 31–September 20, 2016; April 21–May 15, 2017, and on August 29–September 20, 2018, respectively). The bathymetric and spatial patterns of standardized abundance (ind. m^{-2}) and estimated taxonomic diversity (Hill numbers $q = 0$, 1 and 2) were examined. Thirteen environmental variables were measured to characterize the environment, including: organic matter, aromatic and aliphatic hydrocarbons in sediment, bottom water temperature and dissolved oxygen, depth, sediment grain size composition, among others. For analysis, the sampling sites were organized in three depth categories: upper bathyal zone (UBZ, 185–1500 m), lower bathyal zone (LBZ, 1501–3000 m), and abyssal zone (AZ, 3001–3749 m). We collected and identified to family level 684 specimens belonging to 4 orders and 53 Peracarida families in the following order: Amphipoda 19, Isopoda 17, Tanaidacea 13, and Cumacea 4 families. The most abundant Peracarida orders were Amphipoda and Tanaidacea, which represented 36.4% and 35.8% of the total abundance, respectively, followed by Isopoda (25.1%). Cumacea was the least abundant order (2.7%). The ten most abundant families were: Apseudidae, Phoxocephalidae, Caprellidae, Desmosomatidae, Nototanaidae, Nannoniscidae, Tanaellidae, Ischnomesidae, Podoceridae and, Agathotanaidae in order of abundance, which accounted for 66% of the general relative abundance. Abundance decreased with increasing depth showing a significant difference only between UBZ and AZ. The highest abundance values were recorded in the south and the northwest zones of the study area and in the Campeche Bay salt domes area. Intermediate values were also registered in the same regions and in some abyssal localities. The lowest abundance values were particularly recorded in the central region of the study area in the Coatzacoalcos Canyon and abyssal sites. Community structure showed depth-related changes. The main structuring factors of the peracarids communities were: latitude, depth, temperature, and aliphatic hydrocarbons. Diversity based on three estimated Hill numbers consistently decreased with increasing depth. We recorded low diversity values in almost the entire study area, except for the Campeche Bay salt domes zone and northwest region where intermediate and high diversity values were registered.

Key words: Deep-sea, macrofauna, Peracarida, diversity, abundance, Gulf of Mexico

1 Introduction

The Challenger expedition carried out between 1872 and 1876, marked the beginning of the global deep sea explorations (McIntosh, 1885). The efforts of these pioneers were followed by important expeditions: Talisman (France), Albatross (E. U.), and Galathea (Denmark) among others (Gage and Tyler, 1991). Recently, efforts have multiplied and are often carried out at the regional level (e.g., Brandt et al., 2007c, 2018; Wilson, 2017). These investigations tend to focus on the dominant taxonomic groups. Within macrofauna communities (composed by metazoans with a length of less than 1.5 cm that are retained in a sieve with a mesh size between 250 and 500 µm (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 important taxon among the macrofauna (Gage, 2001; Rex et al., 2006) although they have also been recorded as the dominant group (Almeida et al., 2017; Brandt et al., 2019, 2018). These differences are usually the result of the device used to collect the biological samples, however, peracarids are undoubtedly one of the main macrofauna components.

The most abundant and diverse Peracarida orders are the amphipods, isopods and tanaidaceans (Jamieson, 2015). Amphipods are part of the main mobile scavenger fauna. In the hadal zone tens of thousands were reported in traps (Blankenship et al., 2006). The tanaidaceans are one of the most diverse and abundant macrofaunal groups in the deep sea (Larsen, 2005; Wilson, 1987). They are predatory carnivores, detritivores, burrowers or suspensivores, however, many of them are probably opportunistic (Larsen, 2005) and contribute to the rapid utilization of organic matter from the sporadic inputs to the deep sea (Gooday, 1990). Besides, the importance of tanaidaceans as bioindicators of bathymetric zones was pointed out (Hernández-Robles and Escobar-Briones, 2008). Isopods also have been included among the most diverse and abundant Peracarida orders (Angelika Brandt et al., 2007a; Wilson, 1987), and have been registered as more abundant than amphipods (Jennings et al., 2020). Within this order, the suborder Asellota is the most diverse and species rich group inhabiting the deep-sea (Angelika Brandt et al., 2007a; Hartebrodt, 2020; Poore and Wilson, 1993; Wilson, 2008). According to Wilson, (2008), this suborder has the largest number of deep sea representatives with no counterpart in shallow waters. Isopods, also display a variety of feeding habits. They are scavengers, predators, parasites, detritus feeders, and filter feeders and are herbivorous, carnivorous, or omnivorous (Hartebrodt, 2020). So, peracarids play a very important ecological role within the deep sea benthic macrofauna communities. They participate in the bioturbation and bioirrigation sediments processes oxygenating subsurface layers and intervening in the organic matter burial (Crawshaw et al., 2019) promoting bacterial activity and facilitating organic carbon remineralization (Parkes et al., 1994; Snelgrove, 1998; Zhang et al., 2010). Peracarids also get involved in the transport, burial and metabolism of pollutants (Banta and Andersen, 2003; Snelgrove, 1998). They remove pollutants of the water column that can pass through the food chain to another part of the system (Gage, 2001; Snelgrove, 1998). In addition, they affect sediment transport by increasing the susceptibility of the system to erosion (Grant et al., 1982). So, Peracarida constitutes a fundamental component of deep-sea benthic macrofauna communities because it actively participates in global biogeochemical cycles through the nutrients recycling, ecological interactions, and the physical transformation of the environment in which they inhabit.

The abundance and diversity patterns of peracarids have been examined in several studies in different world regions (Błażewicz et al., 2019; A. Brandt et al., 2007; Brandt, 2001, 1997; Brandt et al., 2005, 1997; Brökeland et al., 2007; Di Franco et al., 2021; Frutos and Jażdżewska, 2019; Gage, 2004; Golovan et al., 2013; Rehm et al., 2007), and in various studies in the northern region of the GoM (Larsen, 2005, 2003; Wilson, 2008). Among the contributions, stands out that the most abundant registered order varied depending on the region and particularly with the sampling device used (Almeida et al., 2017; Larsen, 2005). In addition, they highlight groups that have been widely distributed, abundant and diverse in the deep sea, such as the members of the suborder Asellota (Angelika Brandt et al., 2007a; Wilson, 2008) within the isopods and the subfamily Apseudinae within the tanaidaceans (Larsen, 2005). Most of the studies on deep sea peracarids in the Mexican deep waters of the GoM, are related to taxonomic aspects (Escobar-Briones and Winfield, 2003; Ortiz et al., 2022, 2019, 2018; Paz-Rios and Pech, 2021; Winfield et al., 2016, 2006) and those on ecological aspects are scarce (e.g., Hernández-Ávila et al., 2021). The social, economic, and ecological importance of the GoM enhances the need to have a sound knowledge of this large ecosystem that could help to understand its resilience to stressors. The GoM is subjected to chronic and eventual contaminations sources like 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 through (i) evaluate the taxonomic composition of Peracarida macrofauna communities at family level, and (ii) analyze the spatial distribution patterns in the deep sea of the southwestern GoM.

2 Materials and methods

2.1 Study area

The Gulf of Mexico is one of the most productive and diverse Large Marine Ecosystems of the world (Kumpf et al., 1999) bordered by three nations (US, Cuba and Mexico). It has an area of about 1,540,000 km^2 (Ward and Tunnell, 2017) and a maximum depth near to 4000 m in the central area and the Sigsbee Canyon (Darnell, 2015). Most of the GoM (65%) are deep waters of which 42% corresponds to continental slope (200-3000 m) and 24% to abyssal plains (> 3000m) (Ward and Tunnell, 2017). More than a half of its surface area (55%) is Mexican Economic Exclusive Zone. Deep Gulf bottoms are mainly composed of mud from terrigenous and biogenic origin. The Loop Current from the Caribbean Sea determines the Gulf circulation pattern. This current enters through the Yucatán Channel and leaves through the Florida Straits and produces several cyclonic-anticyclonic gyres of different scales depending on the wind and pressure effects (Monreal-Gómez and Salas-de-León, 1997). A general net current flows in a West-North-East direction around the Gulf from Campeche Bank to Florida (Monreal-Gómez et al., 2004). Freshwater is discharged by several rivers around the Gulf among which the Mississippi River in the North and the Grijalva-Usumacinta River System in the South contribute with the highest load.

2.2 Sampling and sample processing

Sediment samples were collected aboard the R/V Justo Sierra of the Universidad Nacional Autónoma de México (UNAM) in the southwest of the GoM during oceanographic cruises SOGOM 1 to SOGOM 4 carried out from June 3–27, 2015; August 31 to September 20, 2016; April 21 to May 15, 2017, and from August 29 to September 20, 2018, respectively. The sampling sites were located within a geographic range of 92.67°–96.70° West longitude and 18.74°–23.04° North latitude, in a depth range of 185 to 3749 m (Fig. 1). The sampling design considered 63 locations on each cruise; however, for logistical reasons only 60, 62, 56 and 62 were successfully sampled from SOGOM 1 to SOGOM 4, respectively. The original numbering of each site was retained for cross-cruise comparisons.

The sediment was collected with a Reineck-type box corer of 0.16 m^2 effective area. A sediment sample of 0.08 m^2 surface and 13 cm depth was collected for faunal analysis in each core. Faunal samples were sieved on board with filtered seawater through a mesh 500 µm size. The taxonomic identification was done using general taxonomic literature (e. g. Kensley and Schotte, 1989; Wetzer et al., 1997; LeCroy et al., 2000; LeCroy, 2002, 2004; Larsen, 2005). Only identified fauna was included in the analysis. The taxonomic names of the organisms were checked against the World Register of Marine Species (WoRMS, www.marinespecies.org). More details of sampling processing can be revised in Quintanar-Retama et al., (2022, 2023).

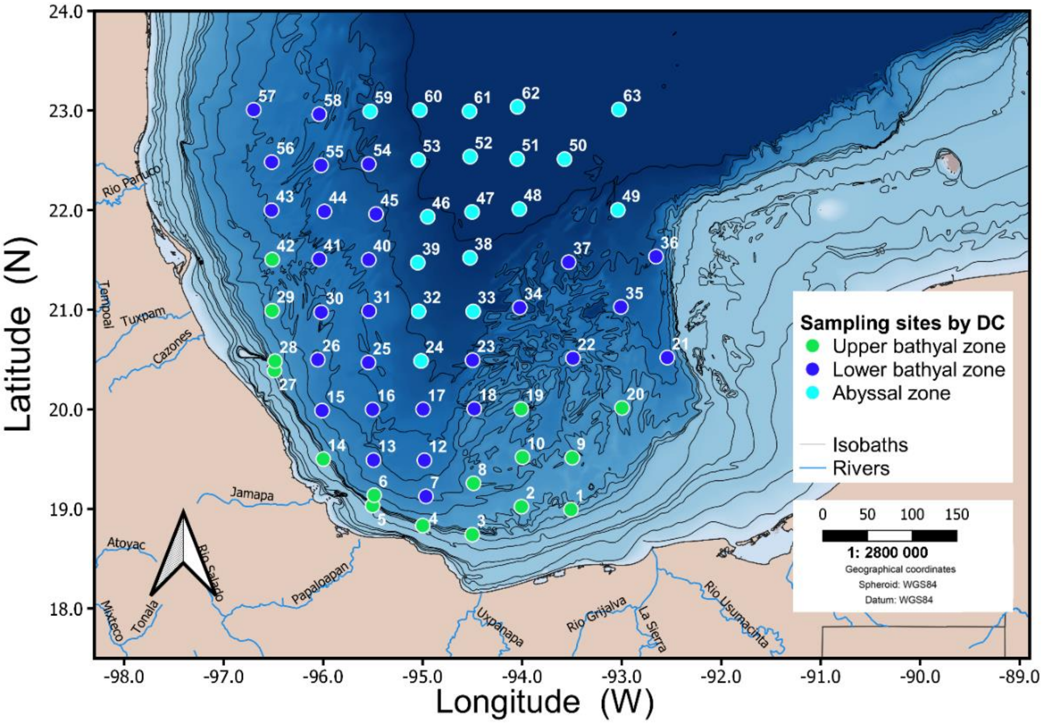


Figure 1. Location of the 63 sampling sites in the oceanographic cruises SOGOM 1-4 Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

2.3 Data analysis

The faunal matrix was elaborated by adding the counts recorded at each site during the four cruises and standardized at ind. m-^{2}. For the environmental analysis, the average of the values obtained in each site was calculated. The sampling sites were organized in three depth categories (DCs): upper bathyal zone (UBZ) (185–1500 m), lower bathyal zone (LBZ) (1501–3000 m), and abyssal zone (AZ) (3001–3749 m). The limit between bathyal and abyssal regions at 3000 m was done based on the literature (e.g., Watling et al., 2013; Harris, 2020) and the GoM bathymetry.

We performed a correlation analysis between the environmental variables to determine which of them covaried. In order to reduce the dimensionality and assess environmental characterizing of each depth category, a principal component analysis was carried out from the environmental variables normalized matrix (removing those that covaried). This was elaborated with R software. For the visualization results we used the pheatmap and factoextra libraries (Kolde, 2019).

Based on the standardized abundance matrices, we constructed box plots to assess possible variations in abundance between depth categories. Also, we did a Kruskal-Wallis test to evaluate the significance of the abundance difference between depth zones. In addition, we constructed percentage and basic stacked bar charts to analyze site-specific bathymetric changes in standardized and relative abundance. The significance between depth and abundance relationship was evaluated with Spearman’s correlation. These were carried out with the ggplot2 library (Wickham, 2016) in R.

Standardized abundance matrix was square root transformed to avoid outlier bias. Subsequently, we generated a pairwise similarity matrix between sites based on the Bray-Curtis index (Clarke et al., 2014) and finally, a non-metric multidimensional scaling (nMDS) with vegan and ggplot2 libraries (Oksanen et al., 2022; Wickham, 2016) in R. In addition, a hierarchical classification analysis (group average) was performed based on the similarity matrix that included the SIMPROF test (1000 permutations for average profile, 999 simulation permutations and 5% level of significance) with clustsig library (Whitaker and Christman, 2014) in R. The classification analysis results were plotted on the nMDS ordering.

Spearman correlations (RS) between biotic and abiotic similarity matrices were calculated using the BIOENV routine (Clarke et al., 2008) with vegan library (Oksanen et al., 2022) in R. The analysis included nine environmental factors (latitude, longitude, depth, temperature, dissolved oxygen, polycyclic aromatic hydrocarbons, aliphatic hydrocarbons, organic matter, and silt). The abiotic factor similarity matrix was generated by Euclidean distances from the environmental variables normalized matrix. Also, we made a heat map to show the possible changes in the composition and structure of the peracarids communities between depth categories with the pheatmap library (Kolde, 2019) in R.

Based on abundance data matrix, we computed diversity estimates (Hill numbers) of order q = 0, 1 and, 2 with the iNEXT library (Chao et al., 2014) in R. The Hill numbers include all three most 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 these three Hill numbers.

The spatial abundance distribution map was elaborated with the standardized abundance values while the spatial diversity distribution map was prepared with the estimated values of taxonomic richness (q = 0) at a 0.8 sampling coverage. All maps were made with QGIS 3.12 software. The aggregation of the sites into classes was carried out with the natural breakage methodology (Jenks) (Smith et al., 2015).

Results

3.1 Environmental analysis

Principal component analysis showed that latitude, organic matter, polycyclic aromatic hydrocarbons, and carbonates concentration in sediments were the environmental variables most related to component one while, longitude and aliphatic hydrocarbons content in sediments were the factors more related to component two. Both components amounted to 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 dissolved oxygen and carbonate content in sediment values. Meanwhile, localities in the upper bathyal region were characterized by the highest bottom water temperature and aromatic hydrocarbons, organic matter and silt content values (Figs. 2, 3, and 4). More details of patterns observed in the measured environmental variables can be consulted in the regional “environmental analysis” section of the manuscript: "Abundance and diversity patterns of Polychaeta families in the southwestern Gulf of Mexico deep waters" which is part of this thesis.

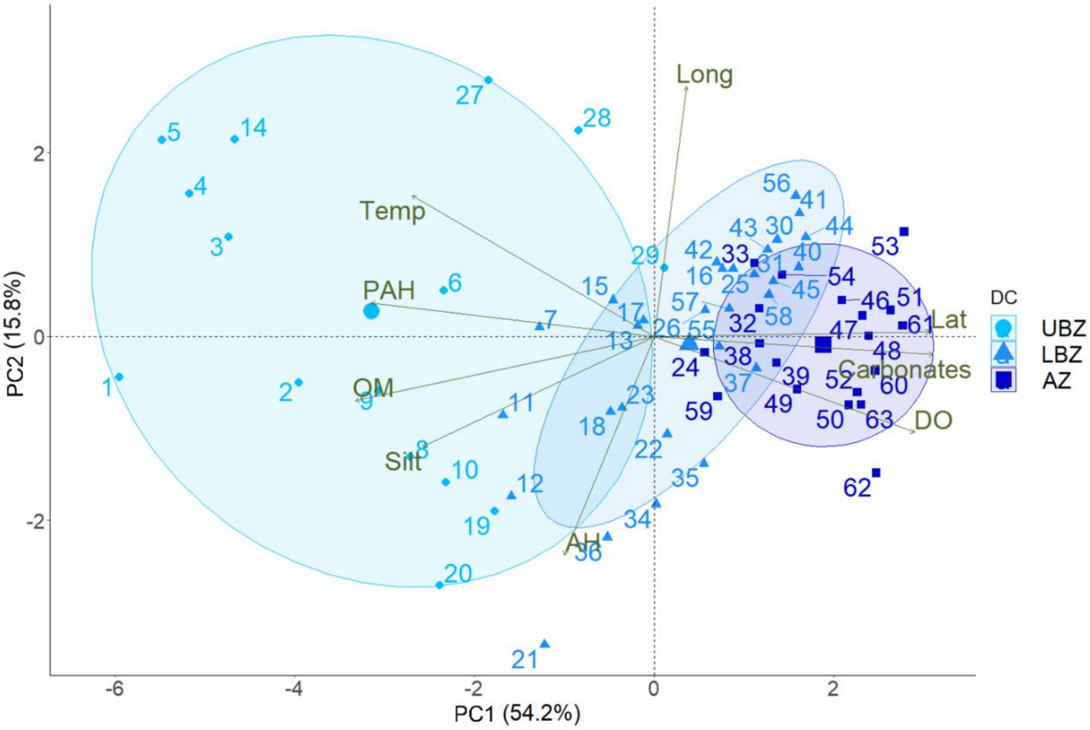


Figure 2. Two-dimensional PCA ordinations on the environmental variables of SOGOM 1-4 PC1 and PC2 accounted for 70% of the variation). Depth category (DC). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

3.2 Fauna description

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

Table 1.

Number of sites, specimens, and families. Average abundance and depth for each depth category.

SOGOM 1-4

Depth category	Number of sites	Number of specimens	Number of families	Average abundance (ind. m^{-2})	Average depth (m)
UBZ	15	227	40	58 (range: 29 -121)	753 (range: 186 -1466)
LBZ	29	326	36	42 (range: 8 - 75)	2293 (range: 1508 - 2545)
AZ	19	131	24	33 (range: 13- 88)	3441 (range: 3018- 3749)

We collected and identified to the family level 684 specimens belonging to 4 orders and 53 Peracarida families in the following order: Amphipoda 19, Isopoda 17, Tanaidacea 13, and Cumacea 4 families (Supplementary data). The most abundant Peracarida orders were amphipods and tanaidaceans, which represented 36.4% and 35.8% of the peracarids total abundance, respectively, followed by isopods (25.1%). Cumaceans were the least abundant order (2.7%) (Fig. 3 a). The ten most abundant families were: Apseudidae, Phoxocephalidae, Caprellidae, Desmosomatidae, Nototanaidae, Nannoniscidae, Tanaellidae, Ischnomesidae, Podoceridae and, Agathotanaidae in order of abundance and accounted for 66% of the general relative abundance (Fig. 3 b). The families which registered most records were: Apseudidae, Phoxocephalidae, Desmosomatidae, Nannoniscidae, and Nototanaidae collected in 40, 38, 30, 27 and 27 sampling sites, respectively. On the other hand, twenty families registered only a single record (Supplementary data).

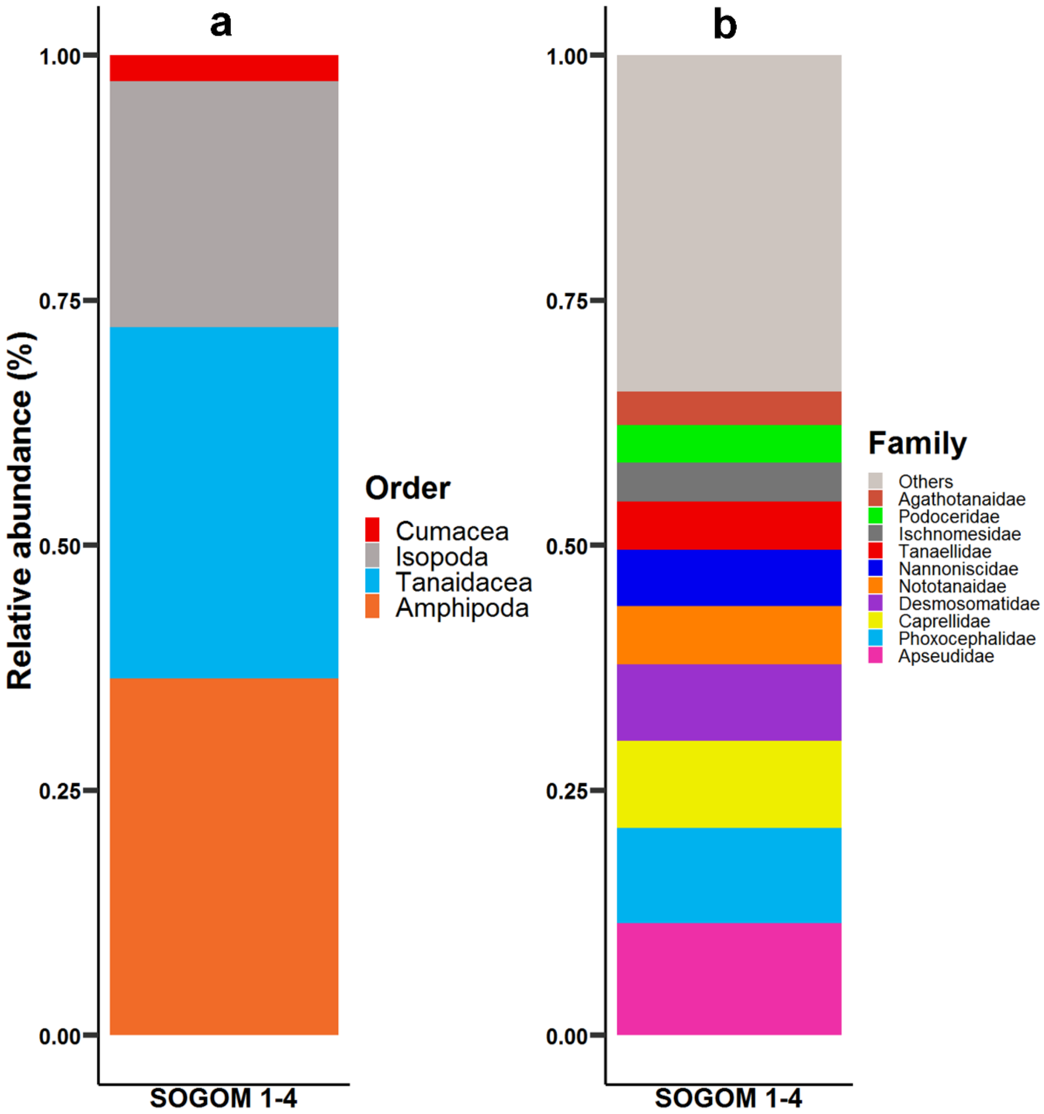


Figure 3 a-b. Relative abundance of the Peracarida during SOGOM 1-4, **a)** orders, **b)** families.

The standardized average abundance was 43 ind. m^{-2} in a range of 8 ind. m^{-2} (site 35 in the Campeche Canyon at 2621 m depth) to 121 ind. m^{-2} (site 6 in the southern region at 1035 m depth).

We observed a decrease of abundance with increasing depth (Figs. 4, and 5), but four sites (56, 58, 23 and 59) registered higher abundance values than adjacent sites in the bathymetric profile (Fig. 5).

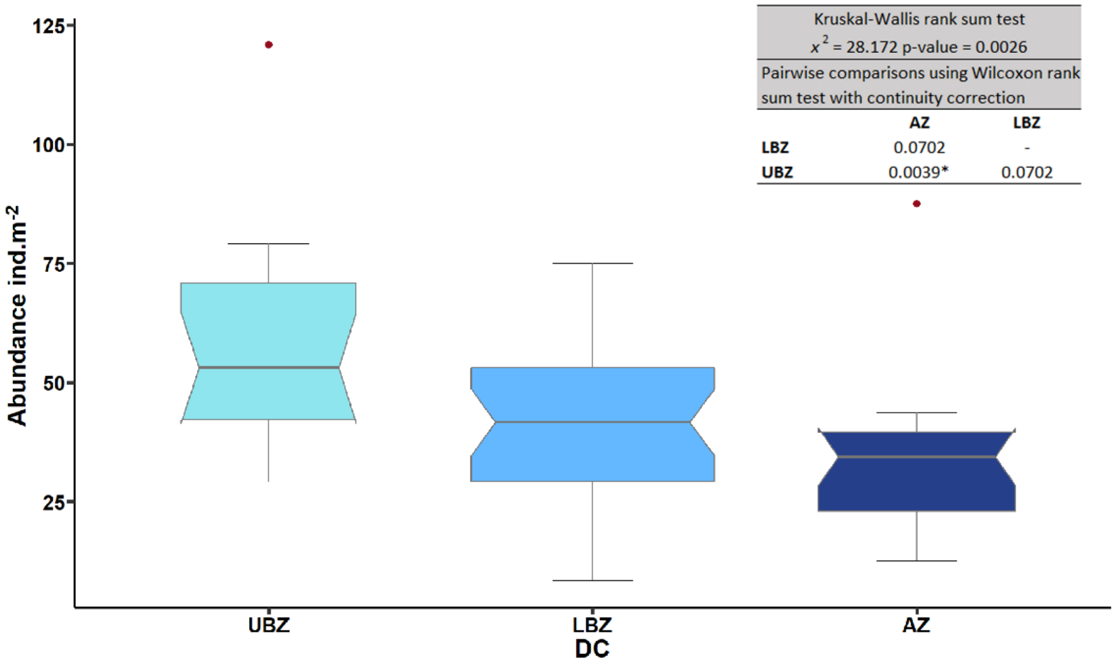


Figure 4. Box plots of Peracarida abundance (ind. m^{-2}) during SOGOM 1-4 Depth category (DC). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

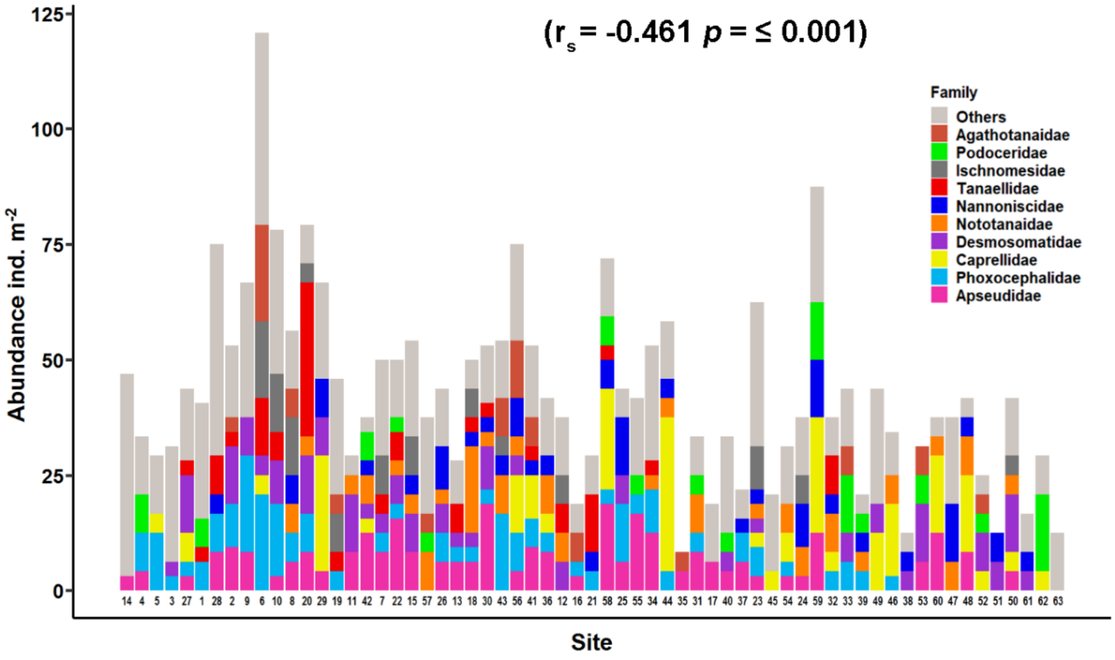


Figure 5. Abundance of the Peracarida families related to depth during SOGOM 1-4. r_s = Spearman correlation. Sites are ordered from shallowest to deepest from left to right.

In general, the highest abundance values were recorded in the south and the northwest regions of the study area and in the Campeche Bay salt domes zone. Intermediate values were registered in the same regions and in some abyssal localities. The low abundance values were particularly found in the central region of the study area in the Coatzacoalcos Canyon and abyssal sites (Fig. 6).

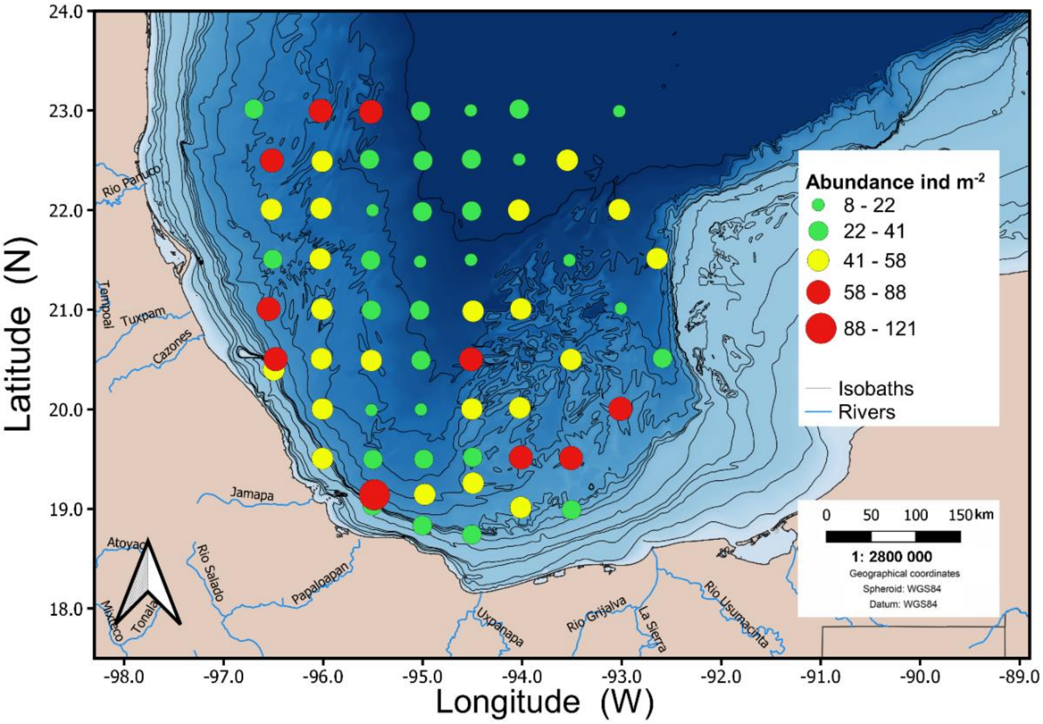


Figure 6. Spatial distribution of Peracarida abundance during SOGOM 1-4.

3.3 Multivariate analysis

The multivariate analysis showed depth-related shifts in the Peracarida community structure. The nMDS showed a gradual composition and structure community variations throughout the analyzed bathymetric range (Fig. 7). The ANOSIM analysis supported these results, as the global value, although relatively low (0.214), was significant (p = 0.001). Besides, the comparison between pairs allowed us to observe the gradual bathymetric variations. All comparison between DCs pair were significative and the highest difference was observed between 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).

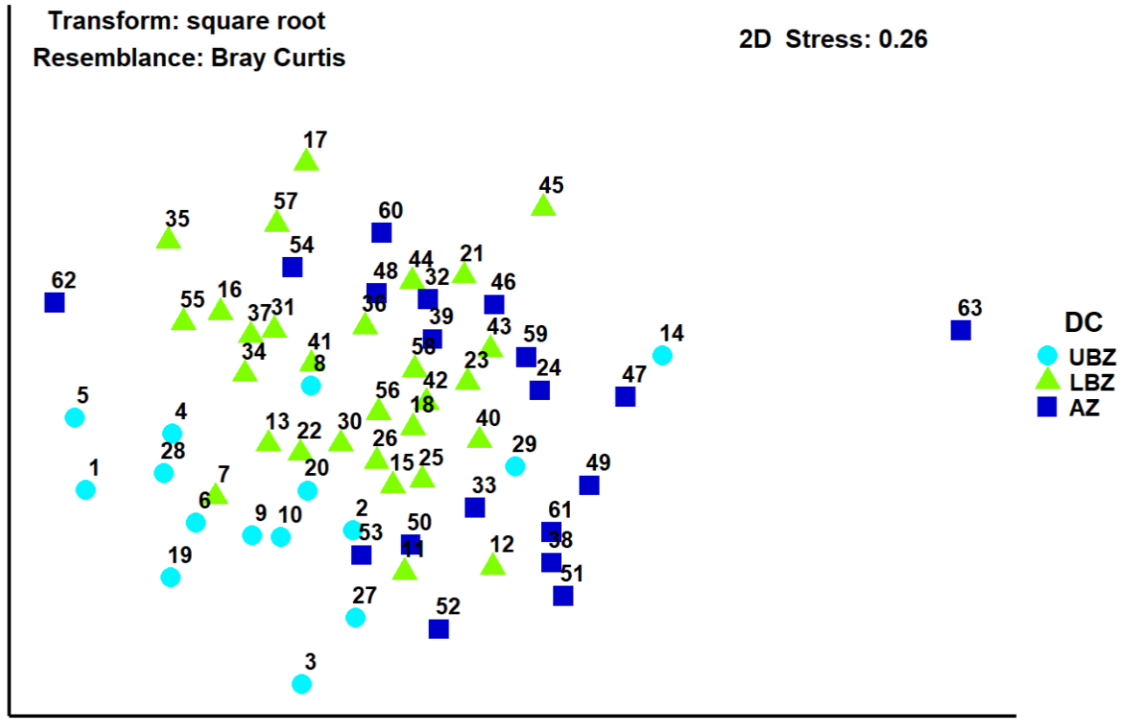


Figure 7. Non-metric multidimensional scaling of Peracarida communities based on Bray Curtis similarities. Depth category (DC). Upper bathyal zone (UBZ-blue circle), lower bathyal zone (LBZ-green triangles), and abyssal zone (AZ-blue square).

The main changes in the Peracarida community structure were due to the best representation of Phoxocephalidae and Ischnomesidae in sites of the upper bathyal region, Apseudidae and Agathotanaidae in localities of LBZ and Desmosomatidae, Caprellidae and Podoceridae in AZ (Fig.8).

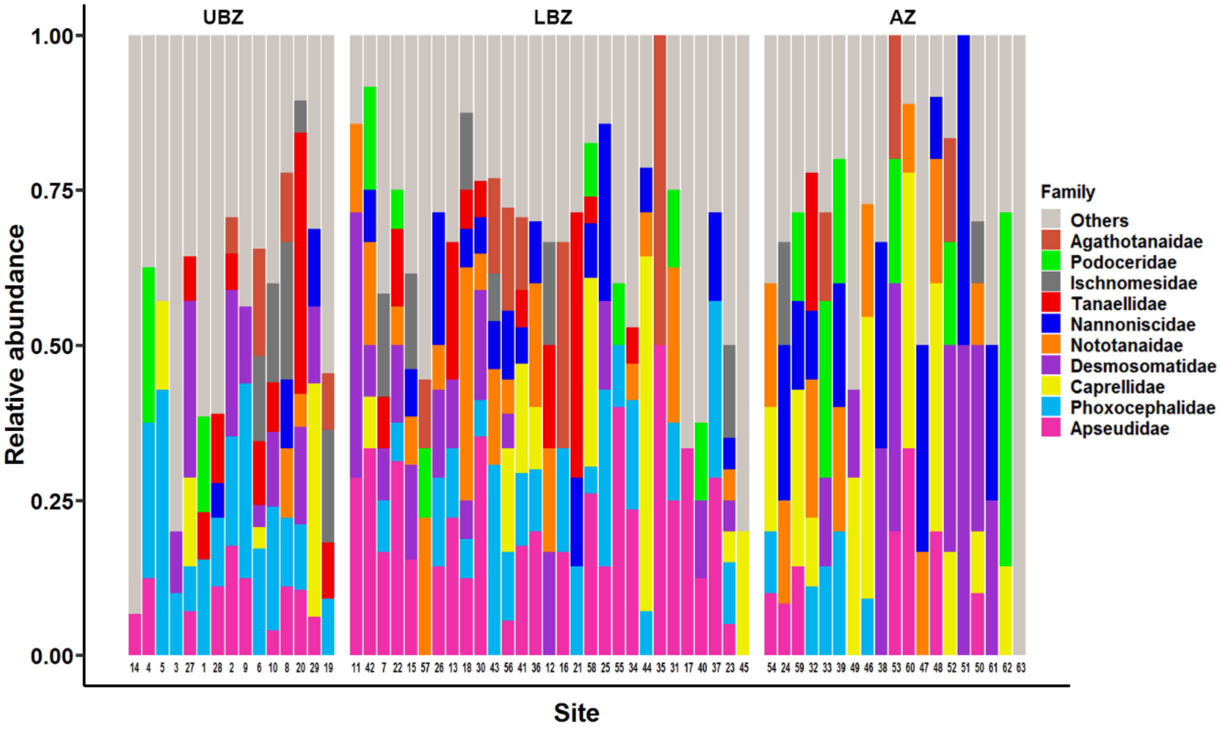
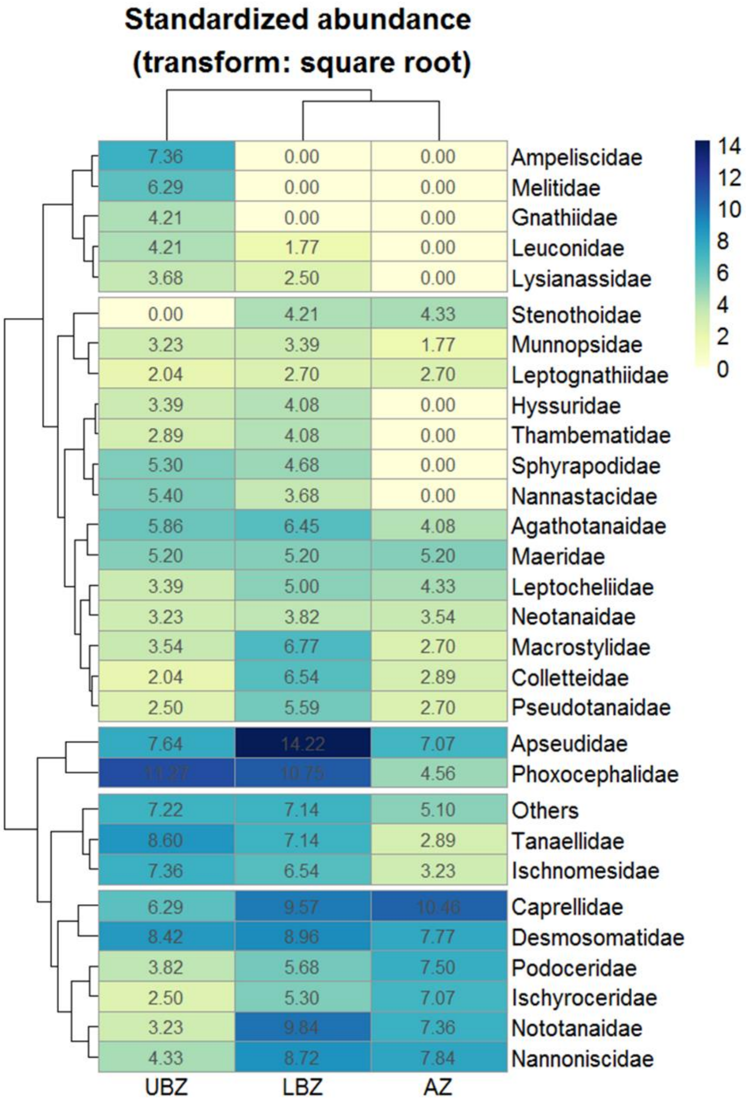


Figure 8. Relative abundance of the Peracarida along depth during SOGOM 1-4. Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ). Sites are ordered from shallowest to deepest from left to right.

The heatmap analysis showed the Peracarida community structure shifts across DCs in standardized abundance terms. The families Phoxocephalidae, Tanaellidae and Ischnomesidae decreased in abundance with increasing depth. The families Apseudidae, Macrostylidae, Colletteidae, Desmosomatidae and Pseudotanaidae presented their highest abundances in LBZ. Meanwhile, the families Caprelidae, Podoceridae, Ischyroceridae, Nototanaidae and Nannoniscidae registered their highest abundances in LBZ and AZ. Finally, Ampeliscidae, Melitidae and Gnathiidae were only recorded in the UBZ while, families Leuconidae and Lysianassidae were collected in the UBZ and LBZ with lower abundances in the last (Fig. 9).



	UBZ	LBZ	AZ
Ampeliscidae	7.36	0.00	0.00
Melitidae	6.29	0.00	0.00
Gnathiidae	4.21	0.00	0.00
Leuconidae	4.21	1.77	0.00
Lysianassidae	3.68	2.50	0.00
Stenothoidae	0.00	4.21	4.33
Munnopsidae	3.23	3.39	1.77
Leptognathiidae	2.04	2.70	2.70
Hyssuridae	3.39	4.08	0.00
Thambematidae	2.89	4.08	0.00
Sphyrapodidae	5.30	4.68	0.00
Nannastacidae	5.40	3.68	0.00
Agathotanaidae	5.86	6.45	4.08
Maeridae	5.20	5.20	5.20
Leptocheliidae	3.39	5.00	4.33
Neotanaidae	3.23	3.82	3.54
Macrostylidae	3.54	6.77	2.70
Colletteidae	2.04	6.54	2.89
Pseudotanaidae	2.50	5.59	2.70
Apseudidae	7.64	14.22	7.07
Phoxocephalidae	11.27	10.75	4.56
Others	7.22	7.14	5.10
Tanaellidae	8.60	7.14	2.89
Ischnomesidae	7.36	6.54	3.23
Caprellidae	6.29	9.57	10.46
Desmosomatidae	8.42	8.96	7.77
Podoceridae	3.82	5.68	7.50
Ischyroceridae	2.50	5.30	7.07
Nototanaidae	3.23	9.84	7.36
Nannoniscidae	4.33	8.72	7.84

Figure 9. Heatmap of the Peracarida abundance. Upper bathyal zone (UBZ), lower bathyal zone (LBZ), and abyssal zone (AZ).

The BIOENV analysis suggested the principal Peracarida community drivers. The combination of environmental parameters (up to 4 factors) that showed the best match with biotic similarity matrices using the Spearman rank correlation were latitude, depth, temperature, and aliphatic hydrocarbons 0.32 correlation (*p* = 0.001) without permuted statistics greater than Rho (Supplementary data).

3.4 Diversity estimators

The diversity analysis showed a 0.94 sampling coverage for the three depth categories. The coverage-based R/E (rarefaction and extrapolation) sampling curves showed UBZ as the depth category with the greatest diversity for the three estimators calculated (Hill numbers, q = 0, 1, and 2) (Fig. 10).

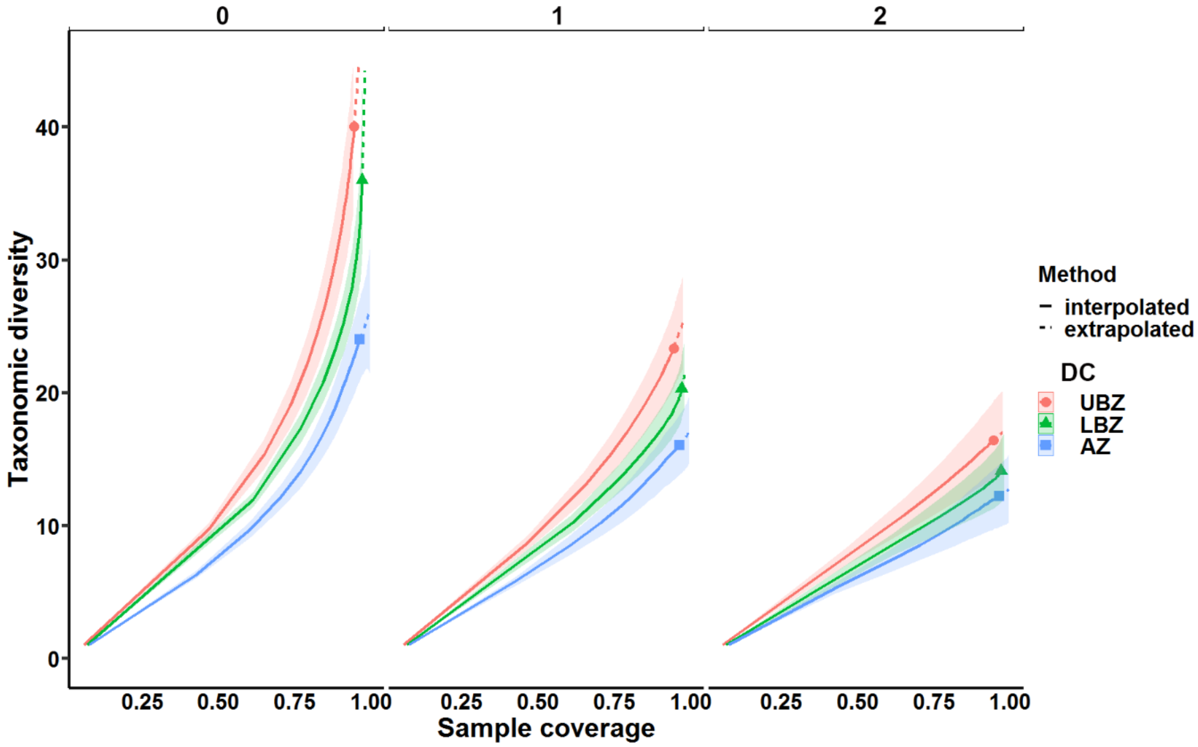


Figure 11. Coverage-based R/E (rarefaction and extrapolation) sampling curves for three Hill numbers (*q* = 0, 1, and 2). Depth category (DC). Upper bathyal zone (UBZ); lower bathyal zone (LBZ) and abyssal zone (AZ).

In general, we observed low diversity values in almost the entire study area, except for the Campeche Bay salt domes zone and northwest region, where intermediate and high diversity values were registered. Besides, one site in the abyssal zone also recorded high diversity values (Fig. 11).

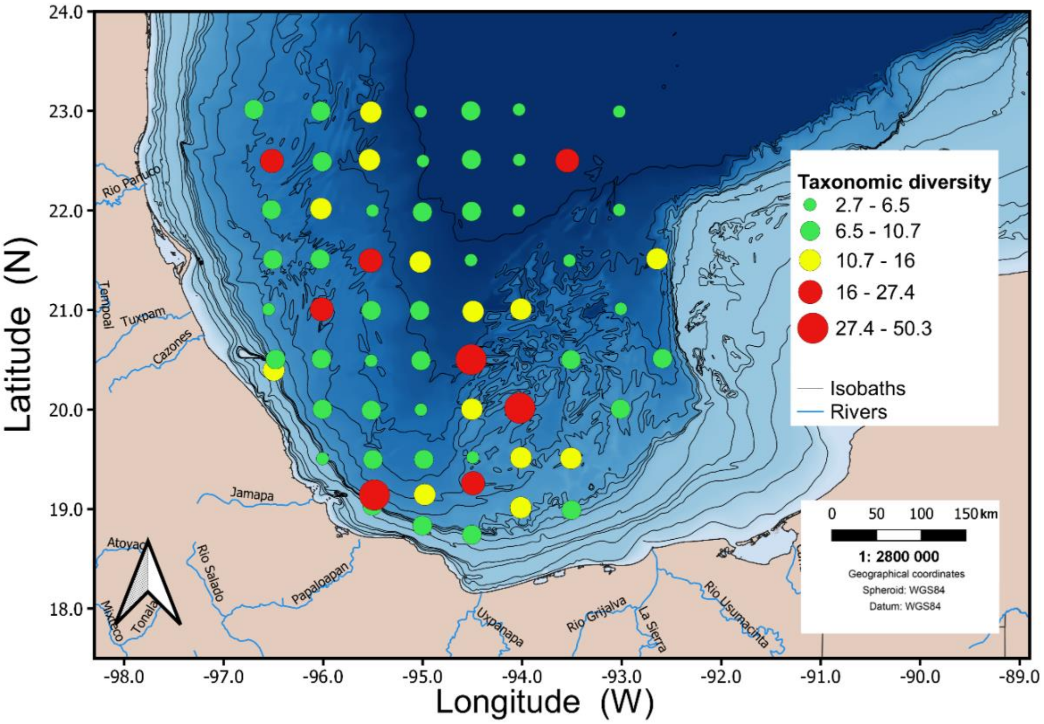


Figure 12. Spatial distribution of Peracarida diversity values during SOGOM 1-4.

3 Discussion

4.1 Environmental analysis

The present study includes the entire bathymetric range of the deep sea (from 200 m) of the southwestern Gulf of Mexico. The environmental characterization showed the zonation of abiotic variables related to depth. In factors such as salinity, dissolved oxygen, and temperature, two zones were observed, one with high variability in UBZ and another (LBZ and AZ), with strong stability in the value of these variables. Besides, a gradual change was observed along the DCs characterized by the highest values of temperature, organic matter, silt and polycyclic aromatic hydrocarbons in UBZ while the AZ showed the highest values of oxygen, clay and the lowest of temperature and organic matter. These patterns of environmental variables have been previously 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 are relevant in the faunal pattern analysis. The variation of productivity, temperature, and diversity of sediment grain size with depth were identified as crucial to determine patterns of abundance, species richness, and their turnover in the deep sea (Joydas et al., 2018; Rex, 1981). A more detailed discussion of the environmental analysis results can be found in section “5.1 Environmental analysis” of the manuscript "Abundance and diversity patterns of Polychaeta families in the southwestern Gulf of Mexico deep waters" which is a chapter of this thesis.

4.2 Fauna description

Amphipoda was the most abundant order in this study which agrees with that reported 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), but this is not a constant rule. Isopoda is usually reported as the dominant order (Brandt et al., 2005; Golovan et al., 2013) and amphipods can be registered among the less abundant orders (Brandt et al., 2005). According to Golovan et al., (2013), the proportion of each peracarids order in the deep sea varies considerably depending on the sampling depth, and the geographical location. Also, it must be considered that the type of sampling device may bias the orders composition. For example, when using an epibenthic sledge, the peracarids are usually the dominant taxon within the macrofauna (Brandt et al., 2005) and the mysids and isopods the most abundant orders (Almeida et al., 2017; Brandt et al., 2005). In our study, the use of the box corer made it difficult to capture groups such as some isopods belonging to the Munopsidae family that have good swimming ability (Angelika Brandt et al., 2007a). Hernández-Ávila et al., (2021) in a study developed in the north of our study area, using the same corer and mesh size for sediment sieving, reported a same ranking in the contribution to total abundance of the Peracarida orders recorded by us (Amphipoda, Tanaidacea, Isopoda and Cumacea).

The ten most abundant families were composed of four tanaidaceans (Apseudidae, Nototanaidae, Tanaellidae and Agathotanaidae), three amphipods (Phoxocephalidae, Caprellidae, Podoceridae) and three isopods (Desmosomatidae, Nannoniscidae, Ischnomesidae). All of them were documented as well-represented taxa in the deep sea (Blazewicz-Paszkowycz et al., 2012; Frutos and Jażdżewska, 2019; Golovan et al., 2013). The most abundant family was Apseudiade. This tanaidacean family is considered the most plesiomorphic and therefore has had time to disperse, adapt and evolve in the bathyal region, mainly the Leviapseudinae subfamily which was only found in the deep sea (at depths higher than 1000 m) (Blazewicz-Paszkowycz et al., 2012). We recorded this family from 186 m in depth. Nototoanaidae and Tanaellidae are well-represented families from the littoral zone to the hadal zone, while Agathotanaidae shows a predominantly abyssal and hadal distribution (Blazewicz-Paszkowycz et al., 2012). On the other hand, Phoxocephalidae and Desmosomatidae are widely distributed, abundant and specious amphipod and isopod families in the deep sea (Brandt et al., 2005, 2007; Wilson, 2008; Golovan et al., 2013). Among the recorded 17 families of isopods, 10 belonged to the Asellota suborder, which was documented as highly dominant in the deep sea (Brandt et al., 2005, 2007; Wilson, 2008). The five families with the highest number of records coincide with the most abundant. Two of them were tanaidaceans (Apseudidae, Nototanaidae), one amphipod (Phoxocephalidae) and two isopods (Desmosomatidae, Nannoniscidae). The family Paranarthrudellidae (Błażewicz et al., 2019) constitutes a new record for the Gulf of Mexico. It is a typical deep-sea cosmopolitan taxon that has not been recorded on the continental shelf. Its range of distribution extends from the bathyal to the hadal region. The closest records to the study area correspond to the North Atlantic. We find this family at a depth of 2,255 m.

We recorded lower abundances values compared to observations made in the north of the GoM. According to Wei et al., (2012), amphipods, tanaidaceans and isopods registered an average abundance of 689 ind. m-^{2} (range 27-16567). We registered an average abundance of 43 ind. m^{-2} (range: 8-121). Data of Wei et al., (2012) indicates the importance of organic carbon discharged by the Mississippi River. If the values of six sites located in front of this river mouth are not considered the average abundance drops to less than half, 315 ind. m^{-2} (range: 27 – 1060). Another factor that should be considered is that the sieving was carried out using a 300 microns mesh size, while we used a 500-micron sieve. Thus, direct comparisons with other studies are not always possible because the devices used to collect the samples are not the same. For example, using an epibenthic sledge is very frequent 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 due to the errors associated with calculating the hauling distance (Brenke, 2005; Brökeland et al., 2007; Golovan et al., 2013).

The general abundance depth related pattern (abundance decreasing when increasing depth) agrees with those previously observed for macrofauna in other seas (Hessler and Sanders, 1968; Gage and Tyler, 1991; Wei et al., 2010, 2012; Baldrighi et al., 2014; Bernardino et al., 2016) (Brökeland et al., 2007; Golovan et al., 2013). This pattern was also recorded in the GoM (Wei et al., 2012) and was related to OM availability with depth

(Morse and Beazley, 2008) and distance from the coast (Escobar-Briones and García-Villalobos, 2009). It is noteworthy that the correlation we observed between the peracarids abundance and depth (cor = -0.39, p = 0.001) was lower than that observed in the same study area with the macrofauna large groups (-0.48 and -0.70, p = 0.001 for both) (Quintanar-Retama et al. al., 2023). However, the peracarid abundance decreasing pattern with depth did not always occur (Brökeland et al., 2007; Golovan et al., 2013).

We registered the highest abundance values in the eastern region, the salt domes zone in the Campeche Bay, and in some intermediate depth sites in the southern region of the study area. This pattern partially coincides with that reported in this region for the macrofauna high level taxa (Quintanar-Retama et al., 2023). 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 Cazones rivers). Meanwhile, the Campeche Bay receives a significant OM amount load from the Grijalva Usumacinta (Toledo-Ocampo, 2005). Furthermore, these sites are in an area where there are a high number of hydrocarbon natural 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 subsequently the OM export to the GoM bottom. These factors together can explain the high abundance values observed in this zone. We recorded the lowest abundance values in the abyssal plain region, an area with lower OM flow (Escobar-Briones and García-Villalobos, 2009) and where we also recorded the lowest values of OM content in sediments.

4.3 Multivariate analysis

ANOSIM and nMDS clearly showed changes in the peracarid community structure and composition across the bathymetric gradient. These results agree with previous studies in other regions (Brandt et al., 2016; Di Franco et al., 2021; Golovan et al., 2013) and in the study area (Hernández-Ávila et al., 2021). The environmental factors that showed high correlation with the peracarid community distribution were latitude and depth. It is important to highlight that both have been registered as structuring factors of deep sea peracarid communities (e.g., Brandt et al., 2007; Di Franco et al., 2021). The third variable most related to fauna was temperature. This is an important benthic communities driver

(Brown and Thatje, 2014) due to its influence on physiological processes (Clarke, 1998) affecting faunal zonation in the deep sea.

With respect to the bathymetric variations of the Peracarida order composition, Cumaceans were only recorded in UBZ and LBZ showing a slight decrease in their relative abundance with increasing depth. The tanaidaceans presented higher relative abundance in LBZ while the amphipods did so in UBZ and AZ. The peracarid families community variations are mainly due to the better Apseudidae representation in LBZ, while, Phoxocephalidae, Tanaellidae and Agathotanaidae were better represented in UBZ and LBZ with a decrease in their relative abundance when increasing depth. Caprellidae, Nototanaidae and Nannoniscidae were better represented in LBZ and AZ. The isopods of the family Desmosomatidae were better represented in UBZ and AZ. According to Frutos and Jażdżewska, (2019), the conditions where caprellids settle are appropriate for filter feeders, while areas with lower proportion of fine sediments are more favorable for infaunal taxa such as phoxcephalids. In UBZ the sedimentation rate is higher than in AZ (Díaz-Asencio et al., 2019) which could imply a less favorable environment for filter organisms, while in AZ it could be the opposite. We recorded an increase in clay and a decrease in silt content related to increasing depth which may favor the establishment of taxa such as Phoxocephalidae in the UBZ region. This could partly explain the distribution of these taxa in our study area.

4.4 Diversity estimators

The order Amphipoda presented the largest number of families which is usually the most diverse within the peracarids (Golovan et al., 2013; Frutos and Jażdżewska, 2019). The ranking of Peracarida orders based on the registered families number (Amphipoda: 19, Isopoda: 17, Tanaidacea: 13 and Cumacea: 4) agrees with that recorded by Golovan et al., (2013). The diversity showed a consistent bathymetric pattern in the three calculated Hill numbers decreasing when increasing depth. These results are also consistent with the reports of Golovan et al. (2013). However, a significant decrease in peracarids diversity is not always recorded with increasing depth (Brandt et al., 1997). Some studies reported high diversity and high number of species with increasing depth (Rehm et al., 2007) or high species richness at intermediate depths between 1,200 and 1,500 m (Wilson, 2008) and around 3,000 m (Brandt et al., 2007a). This is the typical bathymetric diversity pattern in the deep sea (Ramirez-Llodra et al., 2010; Sanders, 1968; Wei and Rowe, 2019) and was recorded in the study area with polychaetes and with higher taxa of the macrofauna (Quintanar-Retama et al., 2023, 2022). However, variations of this pattern were observed depending on the taxon studied. These changes attributable to the region or the target taxon were also previously documented (A. Brandt et al., 2007; Brandt et al., 2009; Shantharam and Baco, 2020).

The diversity (q = 0) spatial distribution values did not show a clear pattern. High values were recorded in the salt domes zone of the Campeche Bay and the southern and northwestern regions of the study area, sites previously documented of high diversity (Quintanar-Retama et al., 2023, 2022), besides a site in the abyssal region. Relative low diversity values were observed in the sites near the coastline and in the Campeche and Coatzacoalcos canyons that could be related with the high sedimentation rate recorded in these sites (Díaz-Asencio et al., 2019). Low diversity and high dominance within peracarid communities has been previously documented in areas with important sedimentary dynamics (Almeida et al., 2017).

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 of the deep-sea peracarid fauna of this poorly studied region. We registered 4 orders and 53 Peracarida families in the following order: Amphipoda 19, Isopoda 17, Tanaidacea 13 and Cumacea 4 families. The most abundant Peracarida orders were amphipods and tanaidaceans, which represented 36.4% and 35.8% of the peracarids total abundance, respectively, followed by isopods (25.1%). Cumaceans were the least abundant order (2.7%). Abundance decreased when increasing depth. UBZ and AZ were significant different, but we did not observe significant differences when comparing adjacent DCs. The highest abundances were recorded in the salt domes zone in the Campeche Bay and in the western and southern regions of the study area. The multivariate analysis showed shifts in the peracarid community composition and structure along the analyzed bathymetric range. The abiotic factors most related to the fauna distribution were: latitude, depth, temperature and sediment aliphatic hydrocarbons content. The bathymetric diversity analysis showed consistent results with the three calculated diversity orders. UBZ being the most diverse, followed by LBZ and AZ the least diverse. The higher diversity values were recorded at some sites located in the southern and western regions of the study area and in the salt domes zone of the Campeche Bay.

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Supplementary material

Abundance matrix

https://docs.google.com/spreadsheets/d/1EfLGRDI_gOTCz7LZLDiOfEVFpiIpFrPf/edit?usp=share_link&ouid=108144172576868121260&rtpof=true&sd=true

Table 1 Taxonomic check list

- Phylum Arthropoda von Siebold, 1848
  - Subhylum Crustacea Brünnich, 1772
    - Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
      - Class Malacostraca Latreille, 1802
        - Superorder Peracarida Calman, 1904
          - Order Amphipoda Latreille, 1816
            - Family Ampeliscidae Krøyer, 1842
            - Family Argissidae Walker, 1904
            - Family Caprellidae Leach, 1814
            - Family Corophiidae Leach, 1814
            - Family Dexaminidae Leach, 1814
            - Family Eriopisidae Lowry & Myers, 2013
            - Family Hadziidae S. Karaman, 1943
            - Family Hyperiidae Dana, 1852
            - Family Ischyroceridae Stebbing, 1899
            - Family Liljeborgiidae Stebbing, 1899
            - Family Lysianassidae Dana, 1849
            - Family Maeridae Krapp-Schickel, 2008
            - Family Melitidae Bousfield, 1973
            - Family Melphidippidae Stebbing, 1899
            - Family Pardaliscidae Boeck, 1871
            - Family Phoxocephalidae G.O. Sars, 1891

  - Family Platyischnopidae Barnard & Drummond, 1979
  - Family Podoceridae Leach, 1814
  - Family Stenothoidae Boeck, 1871
- Order Cumacea Krøyer, 1846
  - Family Diastylidae Bate, 1856
  - Family Lampropidae Sars, 1878
  - Family Leuconidae Sars, 1878
  - Family Nannastacidae Bate, 1866
- Order Isopoda Latreille, 1817
  - Family Anthuridae Leach, 1814
  - Family Chaetiliidae Dana, 1849
  - Family Corallanidae Hansen, 1890
  - Family Dendrotionidae Vanhöffen, 1914
  - Family Desmosomatidae G. O. Sars, 1897
  - Family Gnathiidae Leach, 1814
  - Family Haploniscidae Hansen, 1916
  - Family Hyssuridae Wägele, 1981
  - Family Idoteidae Samouelle, 1819
  - Family Ischnomesidae Hansen, 1916
  - Family Janiridae G. O. Sars, 1897
  - Family Joeropsididae Nordenstam, 1933
  - Family Macrostylidae Hansen, 1916
  - Family Munnopsidae Lilljeborg, 1864
  - Family Nannoniscidae Hansen, 1916
  - Family Protojaniridae Fresi, Idato & Scipione, 1980
  - Family Thambematidae Stebbing, 1912
- Order Tanaidacea Dana, 1849
  - Family Agathotanaidae Lang, 1971
  - Family Anarthruridae Lang, 1971
  - Family Apseudidae Leach, 1814
  - Family Colletteidae Larsen & Wilson, 2002
  - Family Leptocheliidae Lang, 1973
  - Family Leptognathiidae Sieg, 1976
  - Family Neotanaidae Lang, 1956
  - Family Nototanaidae Sieg, 1976
  - Family Paranarthrurellidae Błażewicz, Jóźwiak & Frutos, 2019
  - Family Parapseudidae Gutu, 1981
  - Family Pseudotanaidae Sieg, 1976

Family Sphyrapodidae Sieg, 1976

Family Tanaellidae Larsen & Wilson, 2002

Table 2.
BIOENV results. lat: latitude, temp: temperature, carb: carbonates, sal: salinity, alh: aliphatic hydrocarbons, arh: aromatic hydrocarbons, om: organic matter, th: total hydrocarbons, do: dissolved oxygen.

depth	1	0.2733
lat depth	2	0.3107
lat depth arh	3	0.3162
lat depth temp alh	4	0.3184
lat depth temp arh alh	5	0.3093
lat depth temp arh alh clay	6	0.3053
long lat depth temp arh alh clay	7	0.2986
long lat depth temp arh alh om clay	8	0.2948
long lat depth temp arh alh om silt clay	9	0.2895
long lat depth temp arh alh om sand silt clay	10	0.2804
long lat depth temp do arh alh om sand silt clay	11	0.2723
long lat depth temp do arh alh th om sand silt clay	12	0.2658

Title page

Title: Deep-sea macrofaunal Caudofoveata and Solenogastres (Mollusca, Aplacophora) distribution patterns of southwestern Gulf of Mexico

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Abstract:

Abundance and diversity patterns of Aplacophora collected in 37 sites in the southwestern GoM were analyzed. The study area was located between 92.67°–96.70° W and 18.74°–23.04° N in a bathymetric range of 185 m-3548 m depth. Samples were collected on board the R/V Justo Sierra (Universidad Nacional Autónoma de México) with a Reineck-type box corer during the oceanographic cruises SOGOM 1-4 carried out on June 3–27, 2015; August 31–September 20, 2016; April 21–May 15, 2017, and on August 29–September 20, 2018, respectively. The identification was done at the class and family level. Thirteen environmental variables were measured to characterize the environment, including: bottom water temperature and dissolved oxygen, depth, organic matter, aromatic and aliphatic hydrocarbons sediment content, and sediment grain size composition, among others. The sampling sites were organized in three depth categories: upper bathyal zone (UBZ) (185–1500 m), lower bathyal zone (LBZ) (1501–3000 m), and abyssal zone (AZ) (3001–3749 m) for analysis. We collected and identified to the family level 43 specimens belonging to Caudofoveata class, and 7 specimens identified to class level belonging to Solenogastres. The most abundant taxon was the family Prochaetodermatidae (48% total abundance). The least abundant taxa were Limifossoridae and Solenogastres (14% each). The bathymetric and geographic patterns of standardized abundance (ind. m^{-2}) and taxonomic richness were analyzed. Abundance did not show significant changes among depth categories. The highest abundance values were recorded in the south region of the study area and in the Campeche Bay salt domes zone. Multivariate analysis did not show variations in the community structure related to depth. The main Aplacophora community drivers were: depth, temperature, and sediment grain sizes composition. The highest diversity was recorded in sites near to the coast line in the south region of the study area.

Key words: Deep sea, Aplacophora, Caudofoveata, Solenogastres, diversity, abundance pattern, Gulf of Mexico.

1. Introduction:

The deep sea, deeper than 200 m (Fiege et al., 2010; Gage and Tyler, 1991), is characterized by high hydrostatic pressure, low temperatures and scarce and intermittent food availability (Danovaro et al., 2014; Gage and Tyler, 1991; Ramirez-Llodra et al., 2010). In this area, communities inhabiting hydrothermal vents and hydrocarbon infiltration zones maintain symbiotic relationships with bacteria capable of primary production through chemosynthesis (Demopoulos et al., 2014, 2010; Washburn et al., 2018). Except for these communities, deep sea organisms depend on the organic matter production in the continental region or in surface waters and its subsequent export to the seabed (Biggs et al., 2008; Ducklow et al., 2001; Selvaraj et al., 2015).

Macrofauna is a fundamental component of the deep sea benthic biota and is composed of metazoans with a length of less than 1.5 cm and are retained in a sieve with a mesh size between 250 and 500 microns (Gage, 2001; Hessler and Jumars, 1974; Rex, 1981; Rex et al., 2006) The best studied components in these communities are polychaetes, peracarid crustaceans and bivalve mollusks due to their outstanding abundance and diversity (Allen, 2008; Blazewicz-Paszkowycz et al., 2012; Brandt et al., 2007; Reuscher et al., 2017). Aplacophora usually do not stand out for their abundance but are frequently recorded. This is a small clade of marine shell-less worm-shaped mollusks (Bergmeier et al., 2019; Todt, 2013) with ecological importance due to their habits (Scheltema, 1997). Aplacophores (Solenogastres and Caudofoveata classes) are characterized by a narrow or completely reduced foot and a small mantle cavity restricted to the posterior-most part of the body and by a covered dense coat of spiny or scale-like calcareous sclerites (Kocot et al., 2019; Todt et al., 2008). They have burrowing habits so are involved in sediment bioturbation, and bioirrigation processes that macrofauna communities carried out in the deep sea (Snelgrove, 1998; Zhang et al., 2010). Likewise, they collaborate in the transport, burial and metabolism of pollutants (Banta and Andersen, 2003; Snelgrove, 1998). Also, they intervene in the sinking of organic matter (OM) and oxygen to subsurface layers (Crawshaw et al., 2019) promoting bacterial activity (Parkes et al., 1994), so they actively contribute to nutrient recycling. In addition, they affect sediment transport by increasing the system susceptibility to erosion (Grant et al., 1982).

The aplacophores study is incipient in many regions (e.g., Bergmeier et al., 2017; Ostermair et al., 2018). They are normally included in studies that involve the entire macrofauna community (Brandt et al., 2007; Demopoulos et al., 2014; Girard et al., 2016; Gutt et al., 2016; Wei et al., 2012; Wei and Rowe, 2019) and usually are identified at the Superclass level (Girard et al., 2016; Gutt et al., 2016). This is mainly related to the procedures involved in their taxonomic identification that usually require histological serial sections (Todt, 2013). In the Gulf of Mexico, aplacophores only were mentioned in studies that include the entire macrofauna (Demopoulos et al., 2014; Pequegnat et al., 1990; Wei and Rowe, 2019). But in Mexican deep waters macrofaunal studies are scarce compared to those carried out in the north of the Gulf (but see Escobar-Briones et al., 1999; Wei et al., 2012; Hernández-Ávila et al., 2021, Quintanar-Retama et al., 2023). However, as part of a recent interest in understanding the physical, chemical and biological dynamics of the deep sea of the Gulf of Mexico in the face of possible scenarios of disturbing events in the environment such as oil spills, a significant number of studies have been carried (Murawski et al., 2020; Pulster et al., 2020; Reuscher et al., 2020; Schwing et al., 2020). In this framework, the present study aims to contribute to the knowledge of macrofauna communities through (i) evaluate the taxonomic composition of Aplacophora macrofauna communities at class and family level, and (ii) analyze their spatial distribution patterns in the deep sea of the southwestern GoM. Data obtained from the large bathymetric and geographic range covered in the southern GoM will contribute substantially to the knowledge of macrofaunal communities in this poorly studied area supplying unique information for understanding the GoM as a whole ecosystem. Besides it will provide a baseline data that could be useful to evaluate the impact of man driven activities such as accidental oil spills and/or long-term ecosystem changes.

2. Materials and methods

2.1 Study area

The Gulf of Mexico is one of the most productive and diverse Large Marine Ecosystems of the world (Kumpf et al., 1999) bordered by three nations (US, Cuba and Mexico). It has an area of about 1,540,000 km^2 (Ward and Tunnell, 2017) and a maximum depth near to 4000 m in the central area and the Sigsbee Canyon (Darnell, 2015). Most of the GoM (65%) are deep waters of which 42% corresponds to continental slope (200-3000 m) and 24% to abyssal plains (> 3000m) (Ward and Tunnell, 2017). More than a half of its surface area (55%) is Mexican Economic Exclusive Zone. Deep Gulf bottoms are mainly composed of mud from terrigenous and biogenic origin. The Loop Current from the Caribbean Sea determines the Gulf circulation pattern. This current enters through the Yucatán Channel, leaves through the Florida Straits and produces several cyclonic-anticyclonic gyres of different scales depending on the wind and pressure effects (Monreal-Gómez and Salas-de-León, 1997). A general net current flows in a West-North-East direction around the Gulf from Campeche Bank to Florida (Monreal-Gómez et al., 2004). Freshwater is discharged by several rivers around the Gulf among which the Mississippi River in the North and the Grijalva-Usumacinta River System in the South contribute with the highest load.

2.2 Sampling and sample processing

Sediment samples were collected aboard the R/V Justo Sierra of the Universidad Nacional Autónoma de México (UNAM) in the southwest of the GoM during oceanographic cruises SOGOM 1 to SOGOM 4 carried out from June 3–27, 2015; August 31 to September 20, 2016; April 21 to May 15, 2017 and, from August 29 to September 20, 2018, respectively. The sampling sites were located within a geographic range of 92.67°–96.70° West longitude and 18.74°–23.04° North latitude, in a depth range of 185 to 3749 m (Fig. 1). The sampling design considered 63 locations on each cruise; however only sites with Aplacophora fauna were considered for the analysis.

The sediment was collected with a Reineck-type box corer of 0.16 m^2 effective area. A sediment sample of 0.08 m^2 surface and 13 cm depth was collected for faunal analysis in each core. Approximately 1000 cm^3 of sediment were collected for abiotic parameters measurement. Faunal samples were sieved on board with filtered seawater through a mesh 500 µm size and subsequent fixation was made with a mix of seawater and 8% formaldehyde.

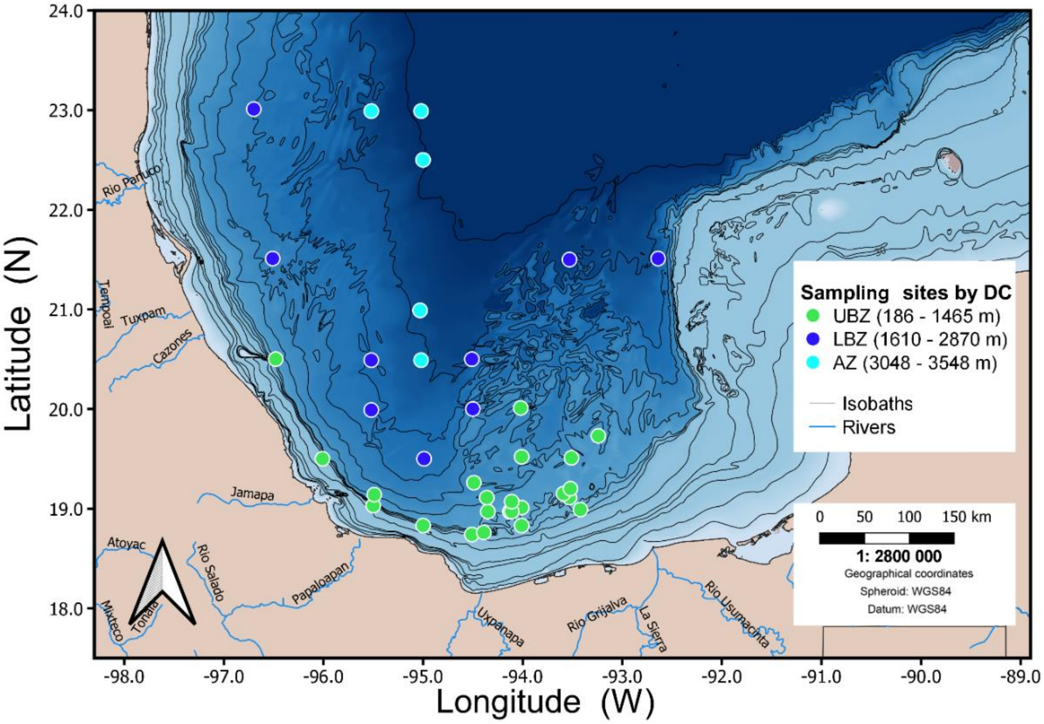


Figure 1. Location of the 37 sites where Aplacophora fauna was registered during oceanographic cruises SOGOM 1-4.

Six of the thirteen abiotic factors were measured in situ. Based on these results, an environmental analysis was done and its relationship with faunal distribution was explored. A detailed description of the sampling process and data analysis methodologies of the environmental data can be found in the “Materials and methods” section of the manuscript: "Abundance and diversity patterns of Polychaeta families in the southwestern Gulf of Mexico deep waters” that is a chapter of this thesis.

In the laboratory, the sediment was examined using an AVEN Mighty Vue Pro 5D ESD magnifying lamp (2.25X magnification). The specimens were picked up with fine point tweezers and preserved in vials with ethanol 70%. Aplacophora specimens were observed under a stereomicroscope Zeiss Stemi 508 (maximum magnification 50X) and Zeiss Primo Star microscope and identified at the family level using general taxonomic literature (e.g., Garcia-Álvarez et al., 2014). Only the identified fauna was included in the analysis. The preservation state allowed to identify only two Solenogastres specimens at the family level (Pruvotinidae). In order not to reduce the number (already scarce) of specimens, all Solenogastres were considered as one more taxon within the analyses.

2.3 Data analysis

The sites of each cruise were organized in three depth categories (DCs): upper bathyal zone (UBZ) (185–1500 m), lower bathyal zone (LBZ) (1501–3000 m), and abyssal zone (AZ) (3001–3740 m). The limit between bathyal and abyssal regions at 3000 m was based on the literature (e.g., Harris, 2020; Watling et al., 2013) and bathymetry of the GoM.

For the environmental characterization of the study area, all the sites (63) with environmental data recorded were included. PCA and Smooth line plots (with 0.3 span) were elaborated with average environmental values for each site.

Due to the small number of specimens, only a regional analysis was performed by adding the counts of the specimens obtained at each of the sites during the four cruises. Based on the standardized abundance matrix (ind. m^{-2}), we elaborated box plots to evaluate possible variations in the aplacophores abundance between depth categories. The plots were made with notches to depict the significance of the possible differences by the overlapping notches (Kampstra, 2008; Mcgill et al., 1978). In addition, we constructed percentage and basic stacked bar charts to analyze the bathymetric changes by site of the aplacophores standardized and relative abundances. The graphs were made with the basic R library. The correlation between abundance and taxonomic richness with depth were analyzed using Pearson's correlation.

The data matrix of standardized abundance by site was square-root transformed to reduce the bias of outliers. Subsequently, a non-metric multidimensional scaling (nMDS) was made on the matrix of pairwise similarity between sites based on the Bray-Curtis index (Clarke et al., 2014). Afterwards we tested differences in the multivariate assemblage structure between depth categories using a one-way similarity analysis (ANOSIM) with 999 permutations. ANOSIM's R-values range from 0 (no differences between groups) to 1 (maximal differences) (Clarke and Gorley, 2015).

Spearman's correlation (RS) between biotic and abiotic similarity matrices were calculated using the BIOENV routine (Clarke et al., 2008). The analysis included eight environmental factors (longitude, depth, temperature, dissolved oxygen, polycyclic aromatic hydrocarbons, aliphatic hydrocarbons, organic matter, and clay). The similarity matrix of abiotic factors was generated by Euclidean distances from the normalized matrix of environmental variables. Multivariate analysis were performed with R (Clarke and Gorley, 2006).

Maps were made to visualize the spatial distribution of standardized abundance and taxonomic richness using QGIS 3.12 software (QGIS.org, 2021). The aggregation of data classes was performed with the natural break methodology (Jenks) (Smith et al., 2015).

3. Results

3.1 Environmental results

Principal component analysis showed that latitude and organic matter, aromatic hydrocarbons and carbonates content in sediments were the environmental variables most related to component one, while longitude and aliphatic hydrocarbons content in sediments were the abiotic factors more related to component two. Both components amounted to 70% of the observed variability. The sites ordered in a bathymetric gradient showed that the abyssal region was characterized by high values of latitude, dissolved oxygen in bottom water, and carbonate content in sediments, while localities in the upper bathyal region were characterized by the highest values of bottom water temperature and aromatic hydrocarbons, organic matter, and silt content in sediments (Fig. 2, and supplementary data). A more detailed results description of the environmental factor analysis can be found in the regional environmental analysis section in the manuscript: "Abundance and diversity patterns of Polychaeta families in the southwestern Gulf of Mexico deep waters" that is part of this thesis.

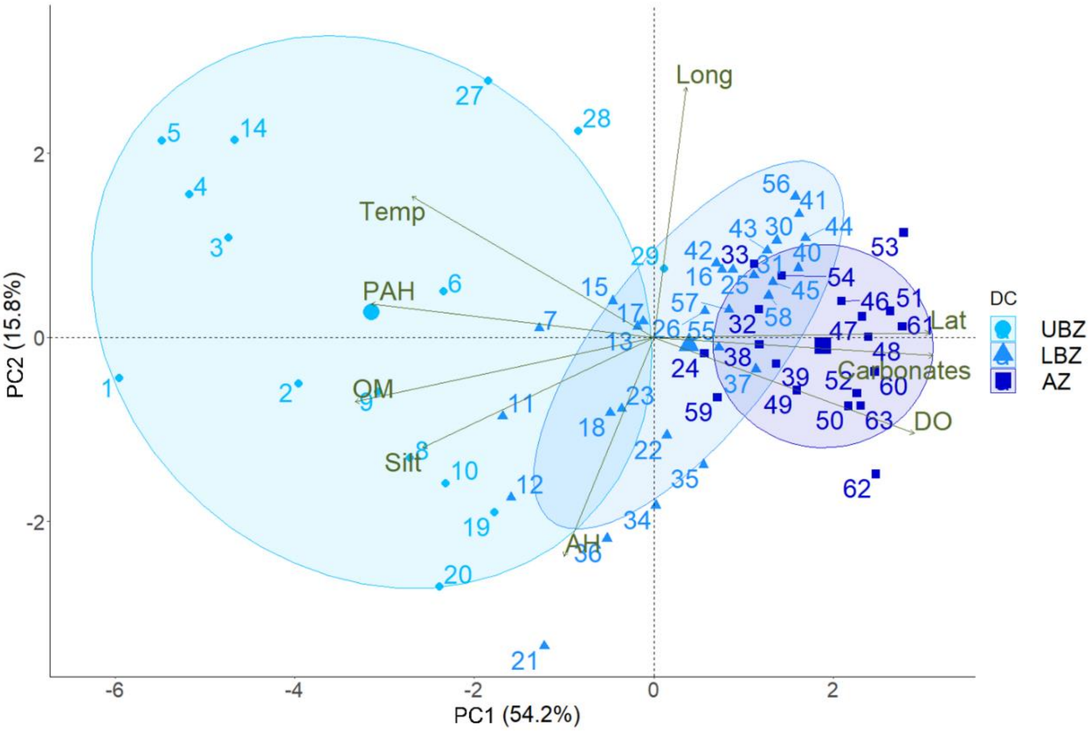


Figure 2. Two-dimensional PCA ordinations of the abiotic factors during SOGOM 1-4 (PC1 and PC2 accounted for 70% of the variation). Depth category (DC). UBZ (Upper bathyal zone), LBZ (lower bathyal zone) and AZ (abyssal zone). Long = longitude, Lat = latitude, DO = dissolved oxygen, Temp = temperature, PAH = polycyclic aromatic hydrocarbons, OM = organic matter and AH = aliphatic hydrocarbons.

3.2 Fauna description

The clustered sites in the UBZ, LBZ, and AZ regions were 23, 9, and 5, respectively. While the number of individuals collected in each of them were: 35, 10, and 5 and the registered taxa 4, 3 and 1, respectively (Table 1).

Table 1.

Number of sites, specimens, and taxa. Average abundance, and depth for each depth category

Cruise	Number of sites	Number of specimens	Number of taxa	Average abundance (ind. m^{-2})	Average depth (m)
UBZ	23	35	4	16.3 (range: 12.5 - 37.5)	685 (range: 186 - 1466)
LBZ	9	10	3	13.9 (range: 12.5 - 25)	2302 (range: 1611 - 2870)
AZ	5	5	1	12.5 (range: 12.5 - 12.5)	3257 (range: 3049 - 3548)

We collected and identified 43 specimens at the family level. Seven specimens were identified to the class level (Solenogastres). Prochaetodermatidae was the dominant taxon with 24 specimens, Chaetodermatidae recorded 12 specimens, and Limifossoridae and the Solenogastres class recorded 7 specimens each. The contribution to the total abundance of each taxon was: 48%, 24%, 14%, and 14%, respectively (Fig. 3).

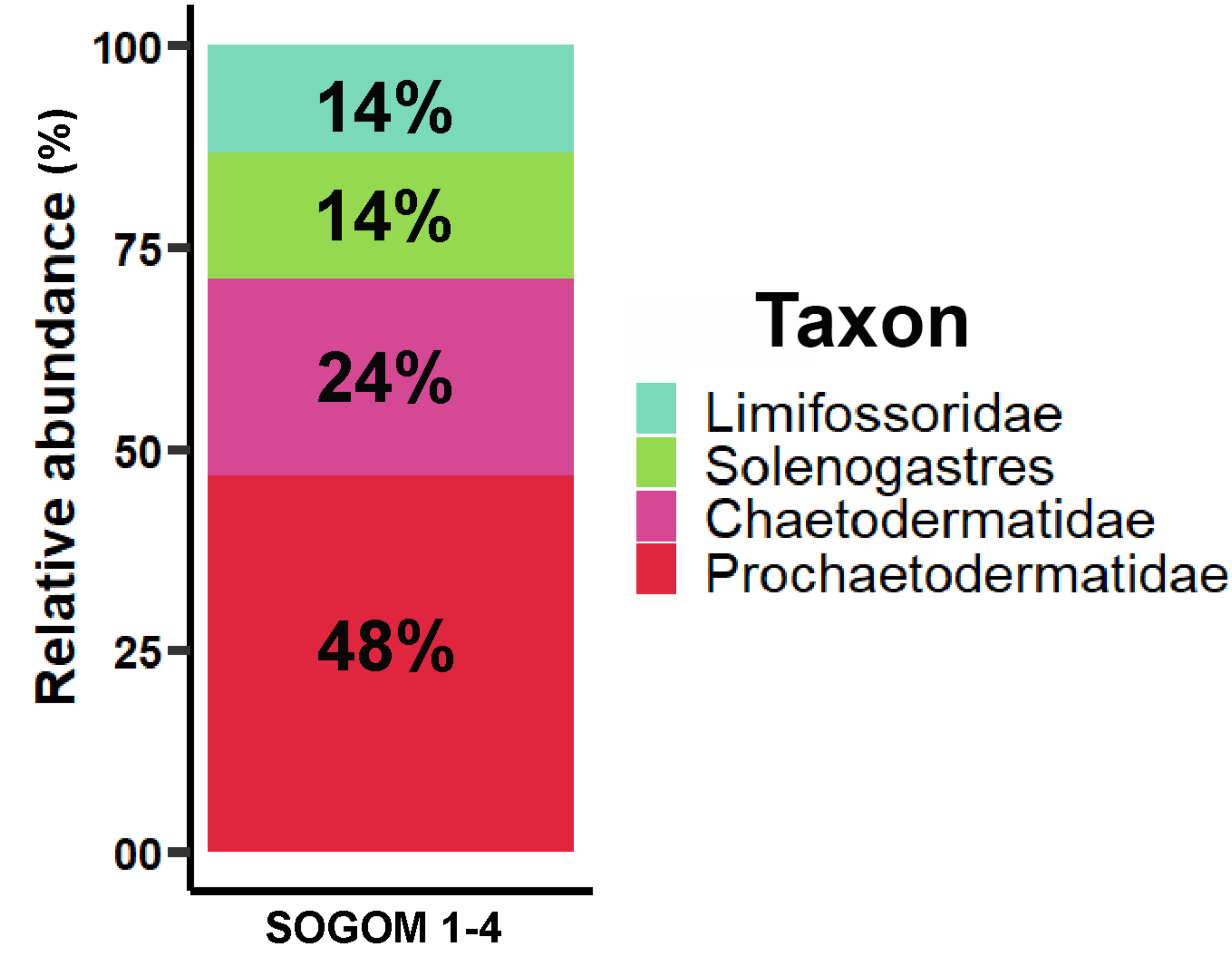
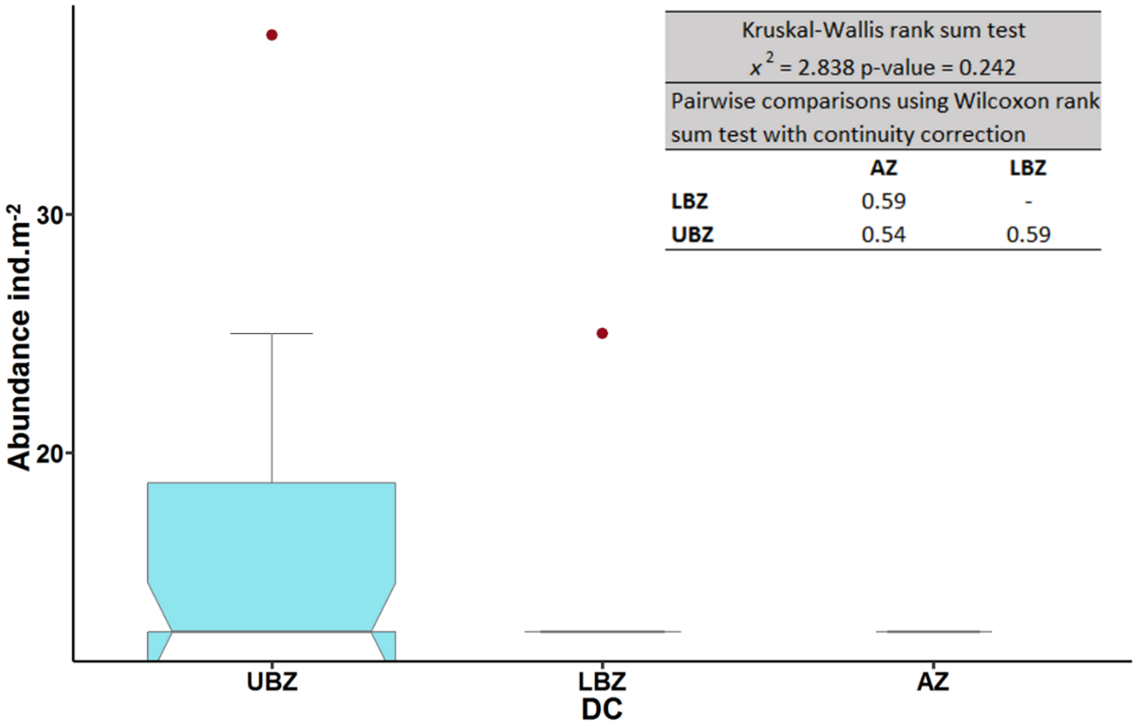


Figure 3. Relative abundance of Aplacophora during SOGOM 1-4.

The average Aplacophora standardized abundance was 15.2 ind. m-^{2} (range: 12.5-37.5). We only registered one and three specimens for each site. We did not record significant correlation between abundance and depth in the entire bathymetric range (r = 0.236, *p* = 0.161) or among DCs (UBZ box notches overlap with LBZ and AZ results (Figs. 4 y 5).



Kruskal-Wallis rank sum test x^2 = 2.838 p-value = 0.242		
Pairwise comparisons using Wilcoxon rank sum test with continuity correction		
	AZ	**LBZ**
LBZ	0.59	-
UBZ	0.54	0.59

Figure 4. Box plots of Aplacophora abundance (ind. m^{-2}) registered during SOGOM 1-4 with Kruskal-Wallis test. Depth category (DC). UBZ (Upper bathyal zone), LBZ (lower bathyal zone) and AZ (abyssal zone).

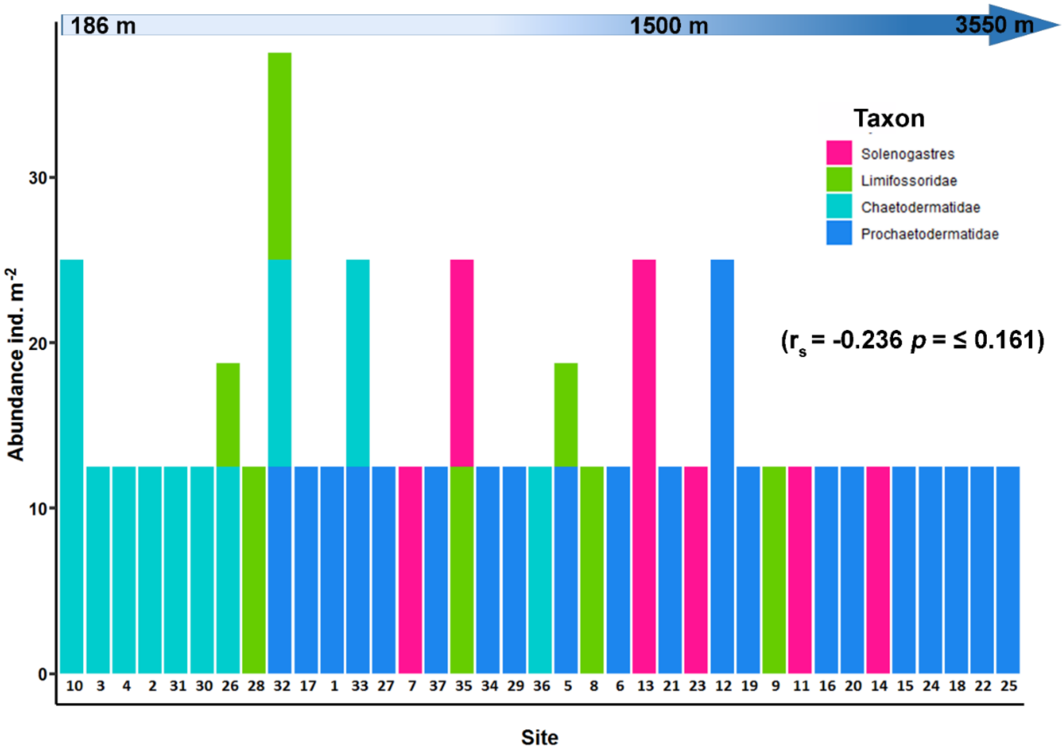


Figure 5. Abundance of the Aplacophora taxa related to depth. Sites are ordered from low to highest depth, left to right. r_s = Spearman correlation. Sites are ordered from shallowest to deepest from left to right.

Intermediate and high abundance values were recorded in shallower sites near the coastline in the southern region of the study area and in the salt domes zone in the Campeche Bay. The rest of the sites showed the lowest value (12.5 ind. m^{-2}) (Fig. 6).

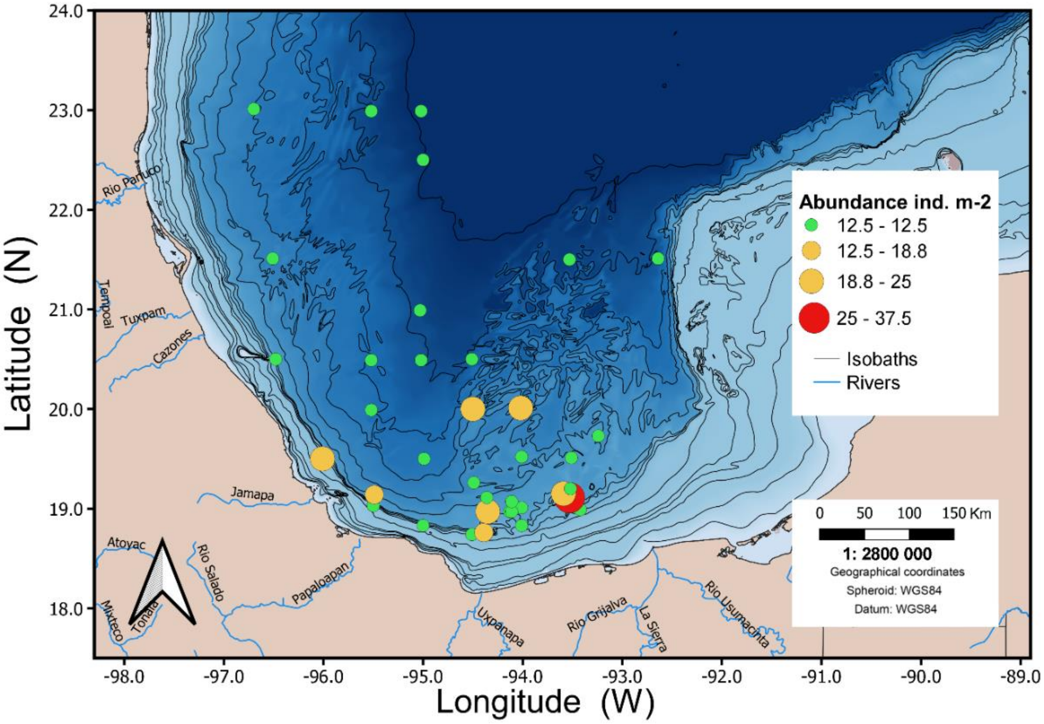


Figure 6. Distribution of the abundance of Aplacophora during SOGOM 1-4.

3.3 Multivariate analysis

The nMDS and ANOSIM analysis did not show clear differences in Aplacophora community structure along DCs (Fig. 7, and supplementary data).

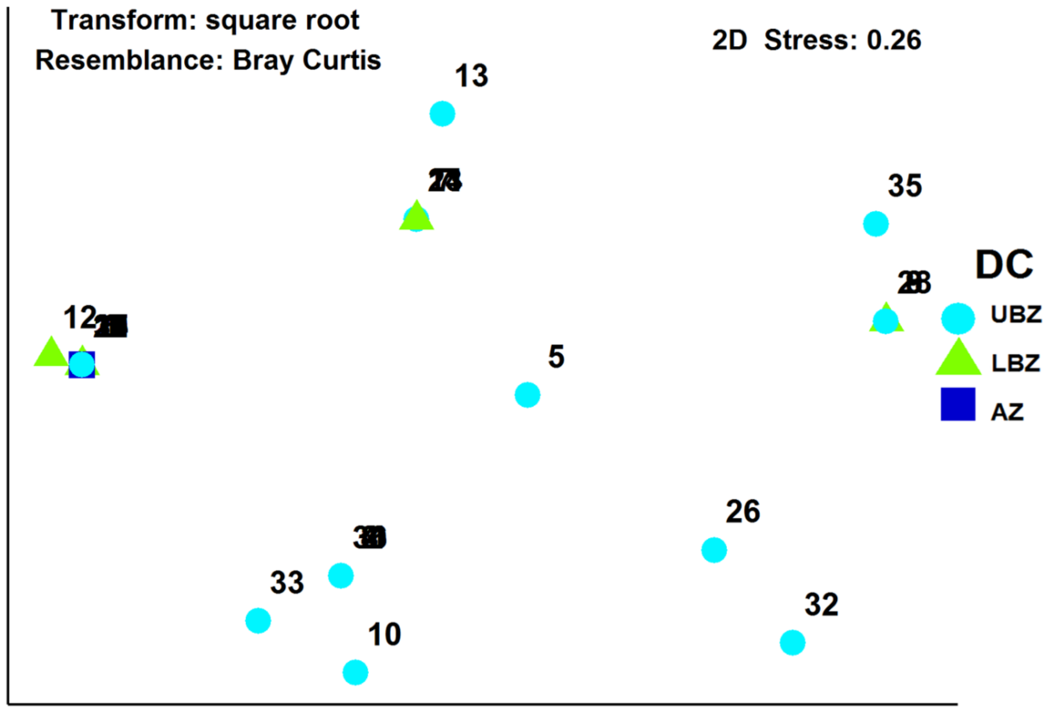


Figure 7. Non-metric multidimensional scaling of Aplacophora community during SOGOM 1-4 based on Bray Curtis similarities. Depth category (DC). Upper bathyal zone (UBZ-blue circles), lower bathyal zone (LBZ-green triangles), and abyssal zone (AZ-blue squares).

The stacked bar graph of percentage contribution to abundance by site neither showed clear differences in the Aplacophora community structure. However, we can highlight that Chaetodermatidae was only recorded up to 1000 m depth and was the dominant taxon up to 500 m depth. In deeper sites this family was not recorded. On the other hand, Prochaetodermatidae was recorded from 600 m to deepest sites and constituted the dominant taxon in this depth interval. The few records of Solenogastres and Limifossoridae were located at intermediate depths (Fig. 8).

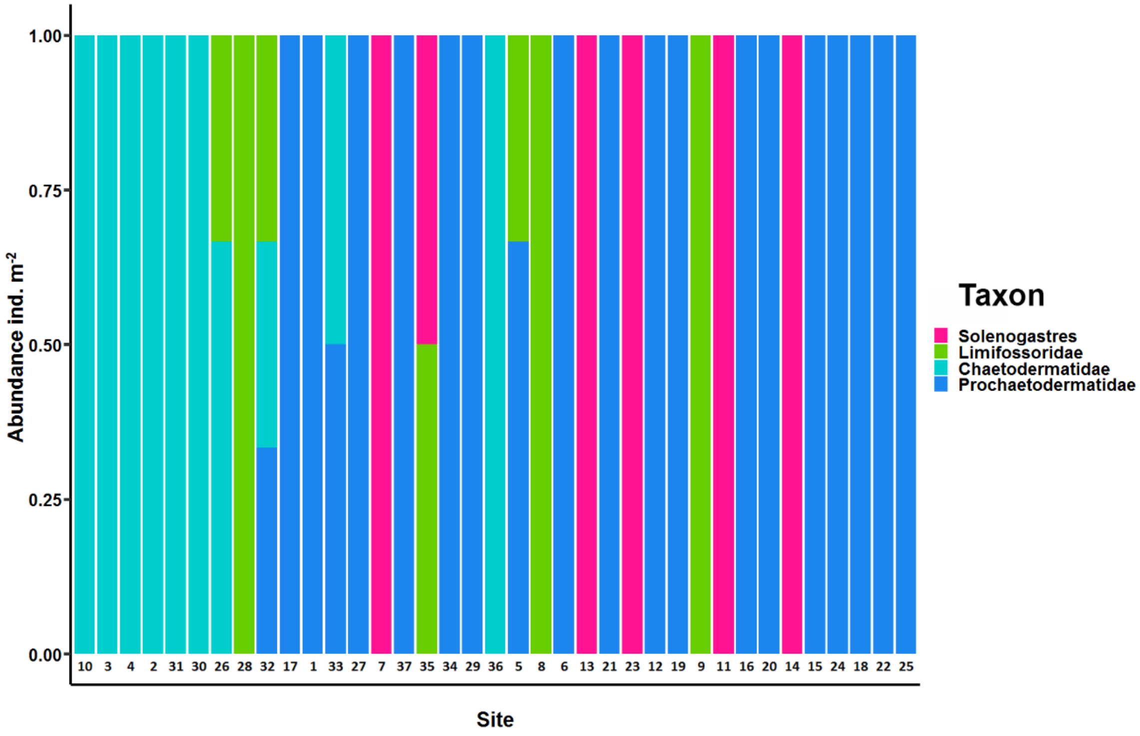


Figure 8. Relative abundance of Aplacophora along depth. Sites are ordered from shallowest to deepest from left to right.

The BIOENV analysis included eight abiotic factors (longitude, depth, temperature, dissolved oxygen, polycyclic aromatic hydrocarbons, aliphatic hydrocarbons, organic matter, and clay). The rest of environmental variables were excluded due to autocorrelation. The environmental parameter combination (up to 4 factors) that showed the best match with biotic similarity matrices using the Spearman rank correlation were depth, temperature and clay with a 0.1779 correlation (*p* = 0.11) with ten permuted statistics greater than Rho. (Supplementary data).

3.4 Diversity estimators

Taxonomic richness showed a negative correlation with depth (-0.2561); however, this was not significant (*p* = 0.1261). Instead, they showed a correlation of 0.77 (p = ≤ 0.001) with the abundance values. Geographically, intermediate (2 taxa) and high (3 taxa) values of taxonomic richness were recorded at shallow sites near the coastline in the southern region of the study area. Only one taxon represented by a single specimen was recorded in 29 of 37 sampled sites.

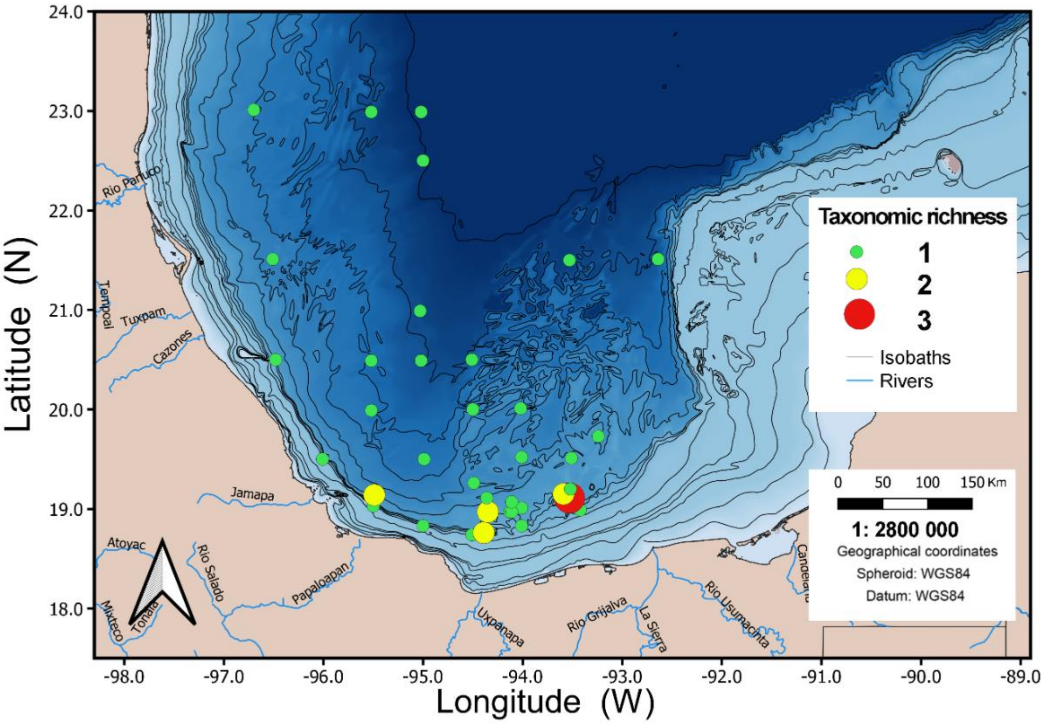


Figure 11. Distribution of Aplacophora taxonomic richness during SOGOM 1-4.

4. Discussion

4.1 Environmental factors

The environmental characterization of the study area showed the gradual change in the abiotic factors throughout the depth interval analyzed. These patterns have been previously documented in the region (Díaz-Asencio et al., 2019; Escobar-Briones and García-Villalobos, 2009; Quintanar-Retama et al., 2022; Rivas et al., 2005). The measured abiotic factors have also been recorded as important structuring of deep-sea benthic communities. Hydrostatic pressure and temperature (Allen, 2008; Brown and Thatje, 2014), oxygen concentration (Levin and Sibuet, 2012), organic matter availability (Bernardino et al., 2016; Brandt et al., 2018; Cosson et al., 1997; Guggolz et al., 2018; Mamouridis et al., 2011), among others. This gradual environmental change registered in the area is important because it could be related to bathymetric changes in the structure of benthic macrofauna communities. A more detailed discussion of the environmental analysis results can be found in section “5.1 Environmental analysis” of the manuscript "Abundance and diversity patterns of Polychaeta families in the southwestern Gulf of Mexico deep waters" which is a chapter of this thesis.

4.2 Fauna description

The aplacophoran community was dominated by Caudofoveata (86% of the total abundance) while Solenogastres represented only 14% of the abundance. Caudofoveata are mainly found in soft sediments, while Solenogastres are epibenthic (partially epizoic lifestyle on their cnidarian prey) or infaunal lifestyle (Todt et al., 2008). The device used to collect the samples could partially explain our results since it is effective for sampling the infauna but not very efficient for collecting epibenthic organisms. In contrast, studies using epibenthic sledges tend to record Solenogastres better than Caudofoveata (e.g., Linse and Schwabe, 2018).

Prochaetodermatidae dominated within Caudofoveata. This taxon that represented 48% of the total abundance, has been documented as typical of the deep sea, along the continental slope. Sometimes it registers high abundance (Corrêa et al., 2018), and constitutes the second most abundant taxon within mollusks (Washburn et al., 2017).

The abundance values that we recorded (range: 12.5 – 37.5 ind. m^{-2}) were lower than those documented in other studies: 40-480 ind. m^{-2} (Scheltema, 1997) 95-1481 ind. m^{-2} (Washburn et al., 2018). However, the mesh size of the sieve, the device used and the depth range in the studies are factors to be considered before making a direct comparison. In this study we used a 500-micron mesh which largely explains the low abundances recorded. This low number of organisms collected may partially explain the non significant abundance difference along the DCs and the no correlation between abundance and depth ($r = -0.2373$, $p = 0.1574$).

Nonetheless, we observed a decreasing trend of aplacophores proportion with increasing depth (73% in UBZ, 31% in LBZ and 26% in AZ of the sampled sites). This agrees with a previous pattern reported where the higher number of species were recorded, between 200 and 1,000 m depth, with very few species after 4,000 m (Todt, 2013). Our results confirm that aplacophores are better represented in UBZ.

We registered relatively intermediate and high abundance values in the salt domes zones of the Campeche Bay. This pattern partially agrees with the results of studies where the macrofauna and polychaetes abundance patterns were examined in this region (Quintanar-Retama et al., 2023, 2022). In this zone, the presence of hydrocarbon seeps has been reported (Sahling et al., 2016) which can maintain chemosynthetic communities with less dependence on surficial layer export OM. Also, a quasi-permanent cyclonic gyre was reported in this area which promotes primary productivity and therefore greater contribution of OM to the seabed (Díaz-Flores et al., 2017). These conditions together may partly explain the higher abundance recorded in the area.

4.3 Multivariate analysis

Although the multivariate analysis did not show a clear pattern in the Aplacophora community along the DCs, the stacked bar percentage plot of the relative abundance, showed a Chaetodermatidae dominance in the UBZ up to 600 m depth and then a Prochaetodermatidae dominance up to the deepest sites. Also, Limifossoridae and Solenogastres presence at intermediate depths was registered. The environmental factors most related to the fauna distribution were depth, temperature and sediment grain size. All of them have been widely documented as benthic communities drivers in the deep sea (Brown and Thatje, 2014; Hernández-Ávila et al., 2021; Levin and Gooday, 2003).

4.4 Diversity estimators

The low abundance values made it difficult to assess the diversity pattern. However, we were able to document that the southern region and the salt domes zone in the Campeche Bay were sites of high diversity. In the study area, a similar behavior was previously reported for polychaetes diversity (Quintanar-Retama et al., 2022). It should be highlighted that taxonomic richness showed a relatively important (0.77) and significant ($p = \leq 0.001$) positive correlation with abundance. In the GoM, 11 species of aplacophores have been recorded (Shantharam and Baco, 2020), all of them in the northwest and none in the southern region. Several studies of the entire macrofauna community in the GoM have reported aplacophores within the best represented taxa (Bourque and Demopoulos, 2018; Pequegnat et al., 1990; Washburn et al., 2016, 2018; Wei et al., 2010; Wei and Rowe, 2019) although some did not register them (Hernández-Ávila et al., 2021). However, not all of them did the identification to the species level. Species identification is based on an analysis combination of the hard parts such as the scleritoma, the radula, copulatory stylets through light or scanning electron microscopy, besides the analysis of soft parts like the genital tract or foregut glands performed through histological sectioning (Bergmeier et al., 2017; Handl and Todt, 2005). So, is a complex and time-consuming task which caused the clade exclusion in biodiversity or biogeographic studies (Bergmeier et al., 2017), or its identification usually done at the Superclass level (Aplacophora) (Girard et al., 2016; Gutt et al., 2016). Efforts focused on external anatomy and on the morphology of isolated hard parts to discriminate between species were carried out (Scheltema and Schander, 2000) however, much of the old (and new) descriptive work is based on histology (Todt, 2013). The use of techniques such as microcomputed tomography to generate three-dimensional internal anatomy reconstructions of specimens and molecular identification techniques could facilitate increased taxonomic resolution (Todt, 2013). This would contribute to the knowledge of this taxon in this region of the Gulf of Mexico.

5. Conclusions

This study constitutes a contribution to establish a base line that could allow subsequent ecological investigations about aplacophores in Mexican deep waters of the Gulf of Mexico. The Solenogastres class and three families of the Caudofoveata class (Prochaetodermatidae, Chaetodermatidae, and Limifossoridae) were recorded. The community was dominated by Prochaetodermatidae (48% contribution to total abundance). The least abundant taxa were Limifossoridae and Solenogastres (14% contribution to abundance of each). Abundance did not show significant differences along DCs or in the continuous depth gradient. The highest abundance values were recorded at sites near the coastline and at shallow depths in the southern region of the study area and at some sites in the salt domes zone in the Bay of Campeche. Even though no significant difference were found in the Aplacophora community structure along the bathymetric gradient, a dominance of Prochaetodermatidae was registered in UBZ up to 600 m depth and from there a dominance of Chaetodermatidae up to the deepest sampling sites. The abiotic factors most closely related to the fauna distribution were depth, temperature and sediment granulometry. In 78% of the sites, only one taxon was recorded. The highest taxonomic richness values were recorded at sites near the coastline at shallow depths in the southern region of the study area.

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Supplementary material

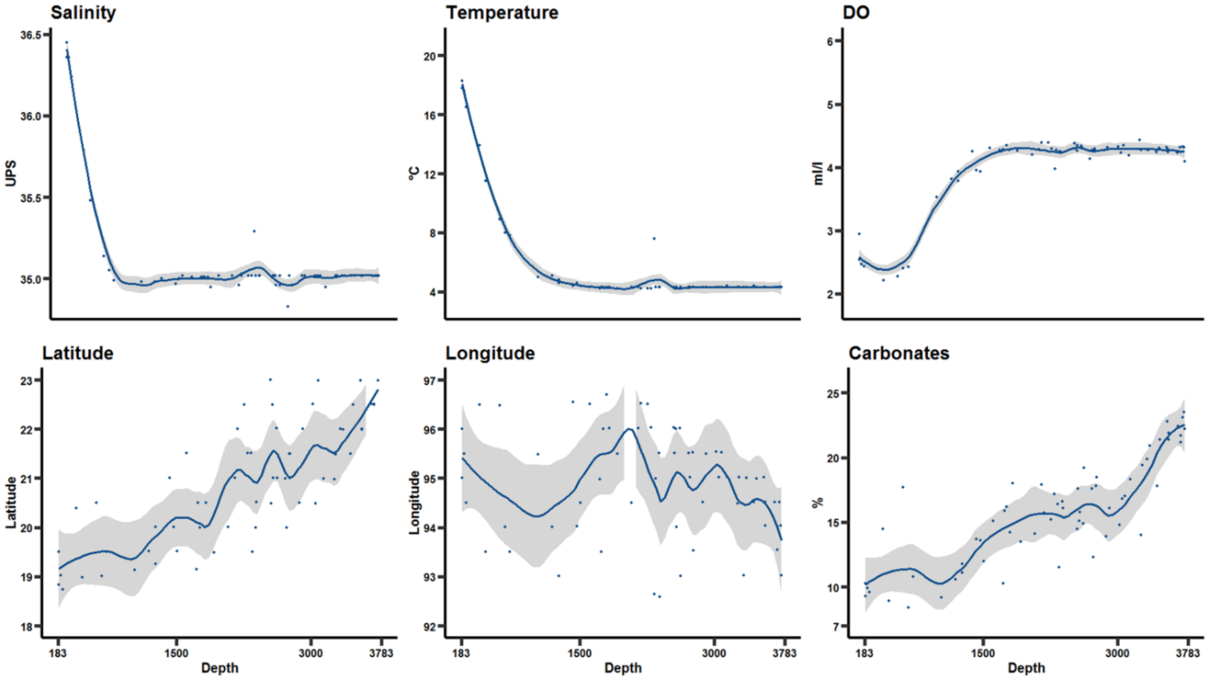

Fig. 1. Depth related pattern of environmental factors. DO = Dissolved oxygen.

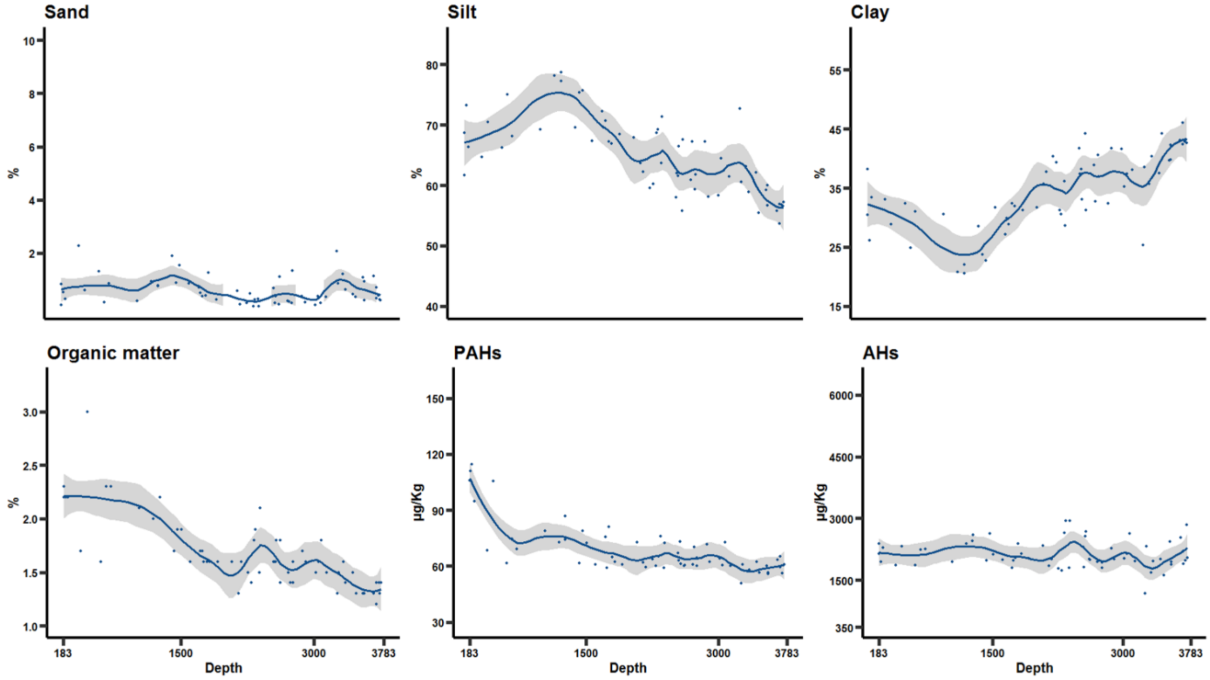

Figure 2. Depth related pattern of environmental factors. AHs = Aliphatic hydrocarbons, PAHs = Polycyclic Aromatic Hydrocarbons.

Table 1.

ANOSIM results

Global test

Sample statistic (Global R): 0.01

Significance level of sample statistic: 36.4%

Number of permutations: 999 (Random sample from a large number)

Number of permuted statistics greater than or equal to Global R: 363

Pairwise Tests

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
UBZ, LBZ	0.073	11.2	28048800	999	111
UBZ, AZ	-0.053	69.6	98280	999	695
LBZ, AZ	-0.048	65.8	2002	999	657

Table 2.
BIOENV results. PAHs: polycyclic aromatic hydrocarbons; Temp: temperature; OM: organic matter; AHs: aliphatic hydrocarbons; Long: longitude; DO: dissolved oxygen.

Significance level of sample statistic: 0.11

Factor (s)	Size	Correlation
PAHs	1	0.1251
Temp Clay	2	0.1717
Depth Temp Clay	3	0.1779
Depth Temp PAHs Clay	4	0.1771
Depth Temp PAHs OM Clay	5	0.173
Depth Temp PAHs AHs OM Clay	6	0.1664
Long Depth Temp PAHs AHs OM Clay	7	0.1578
Long Depth Temp DO PAHs AHs OM Clay	8	0.1454

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Diversity and distribution patterns of macrofauna polychaetes (Annelida) in deep waters of the Southwestern Gulf of Mexico

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ABSTRACT

The distribution and composition at the genus level of polychaetes greater than 500 μm of 54 sites in the southwestern Gulf of Mexico in a depth range of 185–3762 m were analyzed. Samples were collected on board the R/V Justo Sierra (Universidad Nacional Autónoma de México) in two cruises carried out in June 2015 and September 2016. Sixty-nine genera belonging to 33 families were recorded. The families with the highest abundance were: Spionidae, Paraonidae, Pilargidae and Capitellidae. Spionidae, Capitellidae and Paraonidae families presented the highest genus richness. The highest abundance was observed in the southern region of the study area and in the upper bathyal zone while the highest taxonomic richness was registered in the Campeche Bay, in the northwestern region of the study area and in intermediate depths. Polychaeta community functional diversity (bioturbation traits and feeding guilds) was also analyzed. A general decrease in functional diversity was observed as depth increased, presenting a partial biodiffusors and deposit-feeders dominance in the deepest zones. Distribution was highly related with depth, sediment granulometry, temperature and dissolved oxygen concentration of the bottom water.

1. Introduction

Soft-bottom macrofauna communities are composed by metazoans of less than 1.5 cm total length which are retained on a sieve with a mesh size between 250 and 500 μm (Hessler and Jumars, 1974; Rex, 1981; Rex et al., 2006). In the deep sea, a dozen of phyla are typically the most frequent (Grassle, 1991). Among them, polychaete annelids are the best represented with half to three-quarters of the total abundance (Glover et al., 2008; Jumars, 1975; Levin and Gooday, 2003; Qu et al., 2016) followed by peracarid crustaceans and mollusks (Gage, 2001; Levin and Gooday, 2003; Rex et al., 2006).

Due to its high abundance and diversity, Polychaeta is a key taxon for understanding diversity patterns and also a driver in deep sea macrofaunal communities (Grassle and Maciolek, 1992; Olsgard et al., 2003; Olsgard and Somerfield, 2000). Polychaetes play important ecological roles such as decomposition of organic matter, nutrient recycling, and sediment bioturbation (Hutchings, 1998) which are essential for ecosystem functioning (Magalhães and Barros, 2011; Pagliosa, 2005). Besides, they are very useful as indicators of benthic environmental health due to their low mobility and tolerance of some species to environmental stressors (e.g., hypoxia, pollution, and physical reworking) (Dean, 2008; Guerra-García and García-Gómez, 2004).

In their seminal paper, Fauchald and Jumars (1979) focused on the study of the functional diversity of polychaetes and established the trophic guilds for the taxon. Later, many studies addressed to the analysis of polychaete trophic guilds (e.g., Carvalho et al., 2013; Qu et al., 2016, 2017). However, the study of other biological traits such as bioturbation capacity also contribute to the functional assessment of these communities (Bremner et al., 2003).

Bioturbation is defined as all transport processes carried out by animals that directly or indirectly affect the sedimentary matrices (Kristensen et al., 2012). The impact of bioturbation in benthic ecosystems has been evaluated for the macrofauna (e.g., Bouchet et al., 2009; Duport et al., 2007; Valdemarsen et al., 2018) and particularly for polychaetes (Granberg et al., 2008; Maximov et al., 2015). It has been demonstrated that bioturbation has a very important influence on the benthos by increasing the sediment oxygenation (Crawshaw et al., 2019) and fostering microbial metabolic routes related to the organic matter degradation (Quintana et al., 2015).

In the Gulf of Mexico (GM), more than 800 species of polychaetes

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have been recorded, included in more than 300 genera and 60 families (Fauchald et al., 2009). Particularly in the deep-sea area of the GM, about 400 species have been recorded (Pérez-Mendoza et al., 2003; Qu et al., 2016, 2017; Reuscher and Shirley, 2017). However, many of them, referred as "sp." have been not formally described and likely constitute new species.

Most of the studies on polychaete communities have been carried out in the northern deep GM. For instance, analyses of taxonomic and functional diversity patterns (Carvalho et al., 2013); spatial and temporal variations of community structure (Reuscher and Shirley, 2017); the impact of the Deep Water Horizon oil spill (Qu et al., 2016); decadal communities changes (Qu et al., 2017); and influence of productivity on β-diversity patterns (Stuart et al., 2017). However, there are few studies on deep-sea macrofauna communities in the Exclusive Economic Zone of Mexico (but see Escobar-Briones et al., 2008, 1999; Salcedo et al., 2017); and they are particularly scarce on polychaetes (e.g., Pérez-Mendoza et al., 2003). Therefore, there is a big gap of knowledge on the diversity and distribution of polychaete communities in the deep-sea bottoms of Mexican waters. The Gulf of Mexico Research Consortium project (CIGoM) directly targeted this lack of knowledge within its research component "Baseline and Environmental Monitoring" with the goal of establishing oceanographic, biogeochemical, biological, and ecological baselines to assess impacts of potential large oil spills.

The two mega oil spills that occurred in the Gulf of Mexico (Ixtoc 1, 1979–1980 and Deep Water Horizon, 2010) and the increasing trend of deepwater oil industry and its associated potential risks stand out the need to have a sound knowledge of deepwater ecosystem (Pulster et al., 2020; Reuscher et al., 2020; Schwing et al., 2020). The present study aimed to (i) evaluate the taxonomic and functional composition of polychaete communities, and (ii) analyze the spatial distribution patterns in the deep sea of the southwestern GM.

2. Materials and methods

2.1. Study area

The Gulf of Mexico is a semi-enclosed sea bordered by three nations (US, Cuba, and Mexico). It has an extension of about 1,540,000 km^2 (Ward and Tunnell, 2017) and an average depth of 1485 m with a maximum depth near to 4000 m in the central area and the Sigsbee Canyon (Darnell, 2015). About 65% of the GM are deep waters, corresponding 42% to continental slope (200–3000 m) and 24% to abyssal plains (>3000 m) (Ward and Tunnell, 2017). Almost 55% of its surface area belong to the Mexico Economic Exclusive Zone. Deep Gulf bottoms are mainly composed by mud from terrigenous and biogenic origin. According to Davis (2017) there are basically two primary provinces: terrigenous sediments carried from land to the northern and western portions of the Gulf and carbonate sediments that come from the Florida and Yucatán shelves. The Gulf circulation pattern is influenced by the Loop Current that originates in the Caribbean Sea, enters through the Yucatán Channel, and leaves through Florida Straits (Monreal-Gómez et al., 2004). A net current movement West-North-East runs around the Gulf from Campeche Bank to Florida with presence of several cyclonic-anticyclonic gyres of different scales. Several rivers discharge freshwater to the Gulf, but the most important are 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 on board of the R/V Justo Sierra of the Universidad Nacional Autónoma de México (UNAM) in the southwestern GM during the oceanographic cruises SOGOM-1 and SOGOM-2 carried out on June 3–27, 2015 and on August 31–September 20, 2016, respectively. A systematic sampling strategy was designed to cover large gradients in bathymetry, latitude and longitude of the poorly studied area of deep waters of the southern GM. The sampling sites were located within a geographical range of 92.57°–96.69° west longitude and 18.74°–23.02° north latitude, in a depth range from 185 to 3762 m (Fig. 1). The sediment was collected with a Reineck-type box corer of 0.16 m^2 effective area. A sediment sample of 0.08 m^2 surface and 13 cm depth was collected for faunal analysis in each core. Approximately 1000 cm^3 of sediment were collected for measuring abiotic variables. Faunal samples were sieved on board with filtered seawater through a mesh size of 500 μm and subsequent fixation was made with a mix of seawater and 8% formaldehyde. Biological samples are being deposited in the Coleccción Nacional de Poliquetos of the Instituto de Ciencias del Mar y Limnología, of the Universidad Nacional Autónoma de México (CNP-ICML-UNAM).

Four abiotic variables were measured *in situ*. Water depth (m) was determined with the ship's echo sounder. Salinity (PSU), temperature (°C), and dissolved oxygen (ml l^{-1}) in bottom water were measured with a CTD probe (Model Sea-Bird SBE 9 plus). The CTD probe was placed on average at 270 m (range: 16–932 m) from the bottom, depending on the depth site.

In the laboratory, the sediment was examined using an AVEN Mighty Vue Pro 5D ESD magnifying lamp (2.25X magnification). The organisms were picked up with fine point tweezers and preserved in vials with ethanol 70%. Polychaete specimens were observed under a stereomicroscope Zeiss Stemi 508 (maximum magnification 50X) and Zeiss Primo Star microscope and identified at genus level using the general taxonomic literature (De León-González et al., 2009; Fauchald, 1977; Uebelacker and Johnson, 1984) and specialized literature like family revision (e.g., Drennan et al., 2019; Strelzov, 1979) or genus revision (e.g., Sendall and Salazar-Vallejo, 2013; Yokoyama, 2007). However, specimens that were damaged or fragmented could not be identified beyond doubt. The assignment of each genus to a bioturbation category trait was based on Queirós et al. (2013). The assigned categories were: Biodiffusors (B), downward conveyors (DC), upward conveyors (UC), upward and downward conveyors (UC/DC) and surficial modifiers (S). The assignment of feeding guilds was done according to Jumars et al. (2015) proposal.

The content of carbonate was estimated by back titration. Excess hydrochloric acid was used to drive off the carbon dioxide produced in the reaction by boiling and the acid that remains unreacted was titrated with a sodium hydroxide solution, in the presence of the phenolphthalein indicator. Organic matter was estimated through the reaction on one dry gram of sediment with 10 ml of potassium dichromate, 10 ml of sulfuric acid, 100 ml of distilled water and 10 ml of phosphoric acid. One ml of diphenylamine was added, and then organic matter and carbon were estimated based on a titration with a 0.5 N ferrous sulfate (Jackson, 1958). Sediment granulometry was measured using a Beckman Coulter model LS 230 laser diffraction analyzer (Small Volume Modulo Plus), and the particle size distribution was expressed as percentage of sand, silt, and clay.

2.3. Data analysis

We constructed a multiple box plot to compare possible differences of each environmental factor between depth categories with STATISTICA 7 software.

We aggregated the abundance data of the two cruises and later standardized the number of individuals per site. Abundance was standardized to individuals per square meter. Each site was classified into one of four depth categories based on the literature (e.g., Harris, 2020; Watling et al., 2013) and bathymetry of the GM: upper bathyal zone (UBZ) (185–1000 m), middle bathyal zone (MBZ) (1001–2000 m), low bathyal zone (LBZ) (2001–3000 m), and abyssal zone (ABYZ) (3001–3800 m).

We generated matrices with the average abundance of each macrofaunal taxon, polychaete genus, bioturbation trait and feeding guild for each depth category. From these, we elaborated the percentage of contribution to relative average abundance stacked bar charts with

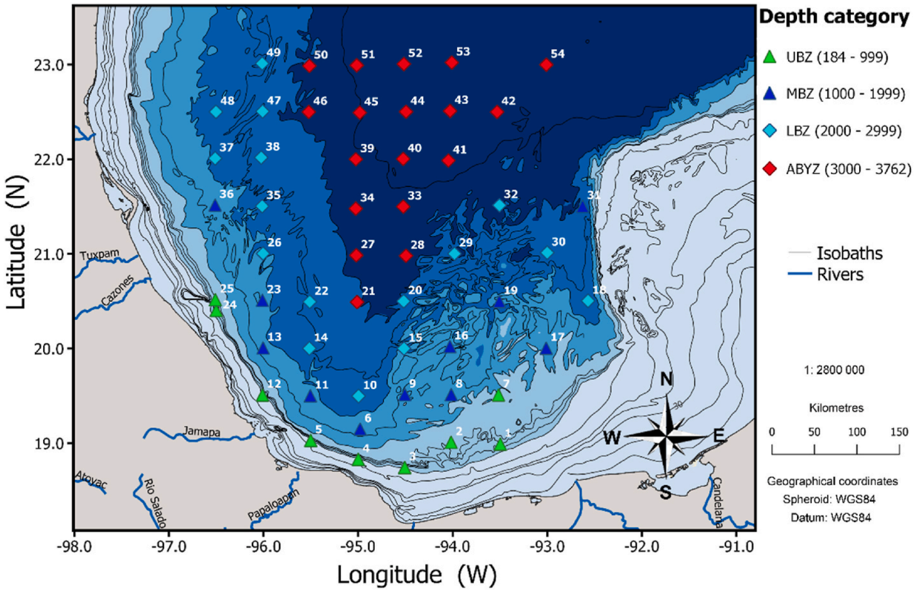

Fig. 1. Location of the 54 sites sampled in the oceanographic cruises SOGOM-1 and 2 in the southwestern Gulf of Mexico. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

STATISTICA 7 software and heat map with gplots 3.1.1 package (Warnes et al., 2020) with R.

The data matrix of standardized abundance by site was square-root transformed to reduce the bias of outliers. Subsequently, a non-metric multidimensional scaling (NMDS) was made on the matrix of pairwise similarity between sites based on the Bray-Curtis index (Clarke et al., 2014). We added a dummy variable (value = 1) to avoid ordering collapse (Clarke et al., 2006). Later we tested differences in the multivariate assemblage structure between depth categories using a one-way similarity analysis (ANOSIM) with 999 permutations. ANOSIM's R-values range from 0 (no differences between groups) to 1 (maximal differences) (Clarke and Gorley, 2015).

A draftsman plot and correlation matrix for environmental factors were calculated to determine the possible covariance between them. The Spearman rank correlations (RS) between matrices of biotic and abiotic similarities were calculated using the BEST routine (Clarke et al., 2008). The abiotic similarity matrix was generated with Euclidean distance from the normalized matrix of environmental variables. All multivariate analyses were carried out with PRIMER v6 (Clarke and Gorley, 2006).

The data matrix of abundance was utilized to compute diversity estimates (Hill numbers) of order $q = 0, 1, 2$ along with the corresponding 95% (conf. = 0.95) confidence interval and plot the coverage-based R/E sampling curves with iNEXT package (Chao et al., 2014) in R. Hill numbers include the three most widely used diversity measures: species richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$). The comparison was carried out through rarefaction at the lower sample coverage registered because it works better to assess the magnitude of the differences in richness among communities (Chao and Jost, 2012).

The geographic distribution abundance map was elaborated with standardized abundance, while the diversity geographic distribution map was elaborated with estimated values of taxonomic richness ($q = 0$) at the lower sample coverage observed (0.75). The geographic distribution maps of sample sites, abundance and genus richness were made with the QGIS 3.12 software (QGIS.org, 2021).

3. Results

Depth grouping sites resulted in 9, 11, 16, and 18 locations for UBZ, MBZ, LBZ and ABYZ, respectively. The highest number of genera and specimens were registered in the UBZ while the lowest was observed in the ABYZ (Table 1).

Three of the measured environmental parameters showed remarkable difference between UBZ and the three deepest zones. The parameter ranges (regardless of outliers) in these two sites groups were: Temperature (18.65 °C–7.79 °C) - (4.97 °C–4.24 °C); salinity (36.43 PSU- 35.00 PSU) - (34.98 PSU- 34.94 PSU) and dissolved oxygen (2.60 ml l^{-1}- 2.12 ml l^{-1}) - (4.28 ml l^{-1}– 4.09 ml l^{-1}). Besides, the silt clay ratio and organic matter showed a decreasing pattern with the highest values in the UBZ and lower in the ABYZ (3.07 %–1.34%; 2.38 %–1.26%, respectively), whereas carbonates registered an inverse gradient with the lower value (8.0%) in the UBZ and the highest one (24.24%) in the ABYZ (Fig. 2).

Sixty-nine genera of Polychaeta belonging to 33 families were collected. The best represented families (number of genera in parenthesis) were Spionidae (7), Capitellidae (5), Paraonidae (5), Ampharetidae (4), Lumbrineridae (4), Opheliidae (4), Cirratulidae (3), Goniadidae (3), and Pilargidae (3). Seven families were represented by two genera and 17 families had a single genus. Spionidae, Paraonidae, Pilargidae, Capitellidae and Longosomatidae were the more abundant families.

Polychaeta contributed with 25–48% to total macrofauna average abundance. In general, Polychaeta abundance showed a decreasing

Table 1
Number of sites, range and average depth, families, genera and specimens by depth categories.

Depth category	Number of sites	Average depth (m)	Number of families	Number of genera	Number of specimens
UBZ	9	397 (range: 184–769)	22	39	145
MBZ	11	1641 (range: 1205–1916)	20	32	67
LBZ	16	2449 (range: 2080–2875)	22	30	55
ABYZ	18	3451 (range: 3027–3762)	17	20	43

Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

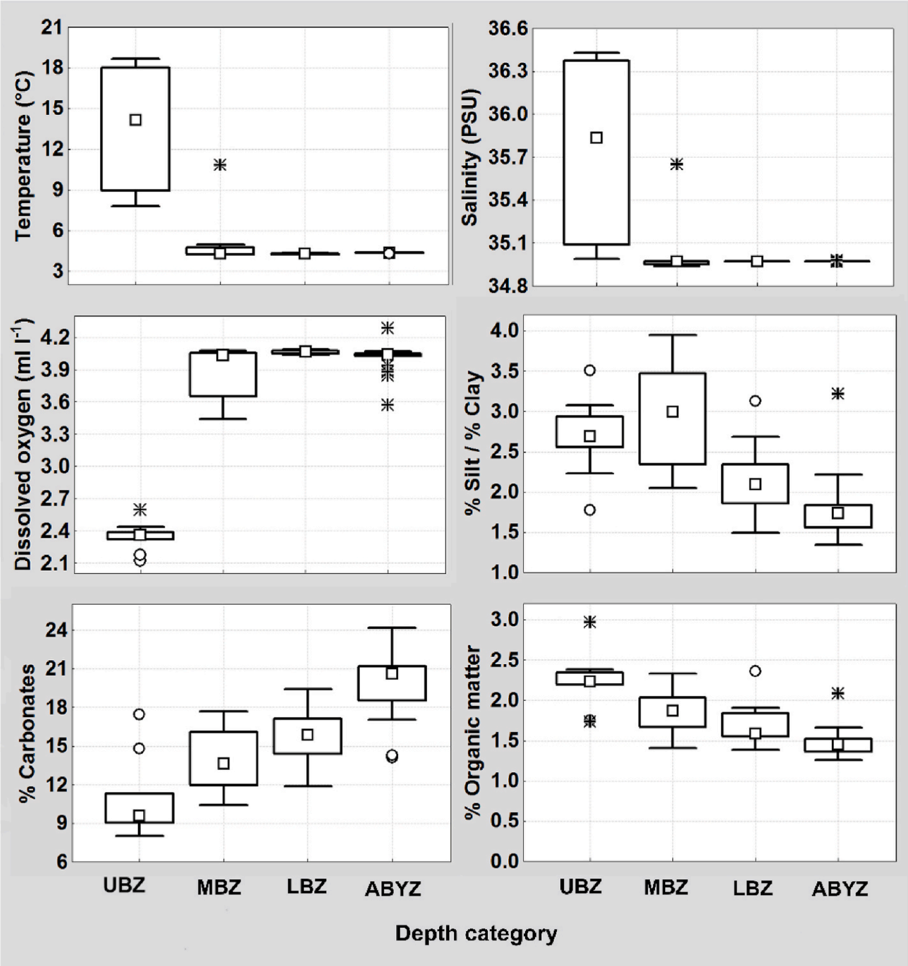

Fig. 2. Box plots of environmental factors by depth category. □ Median; ☐ 25%–75%; ⌶ Non-Outlier Range; O Outliers; * Extremes. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

pattern with depth increase. The highest contribution was registered in the UBZ and the minor one in the LBZ. Sipuncula, Amphipoda and others (taxa with less than 2.4% contribution to total abundance) registered the highest contribution in the UBZ and minor one in the deepest zones. On the other hand, Porifera, Bivalvia, Tanaidacea, Isopoda and Harpacticoida recorded the highest contribution in the deepest zones compared to the UBZ (Fig. 3).

The most abundant polychaete genera were *Levinsenia* Mesnil, 1897, *Prionospio* Malmgren, 1867, *Paraprionospio* Caullery, 1914, *Heterospio* Ehlers, 1874, and *Aricidea* Webster, 1879. The genera with the highest occurrence were: *Heterospio* Ehlers, 1874, *Levinsenia* Mesnil, 1897, *Aricidea* Webster, 1879, *Sigambra* Müller, 1858, and *Notomastus* M. Sars (1851). Thirty-three genera had only one register and 30 of them registered the lowest abundance (6.25 ind. m^{-2}). The highest abundance was found in the UBZ and sites near the southwestern coast of the study area (Fig. 4). Also, we observed two groups of stations with relatively high abundances that do not strictly fit to the general pattern registered. One group of sites 8, 9, 15, 16, 17, 19, 29, and 32 (group A) located on the Campeche Bay and another with sites 39, 40, 45 and 51 (group B) on the continental rise. In general, the lowest abundance values were observed in the LBZ, ABYZ, and in the northern region of the study area.

According to the NMDS analysis based on standardized genera abundances; sampling sites were ordered along a bathymetric gradient. Upper bathyal sites separated from the abyssal ones, whereas locations of the MBZ and LBZ mixed with those of the other two bathymetric zones (Fig. 5).

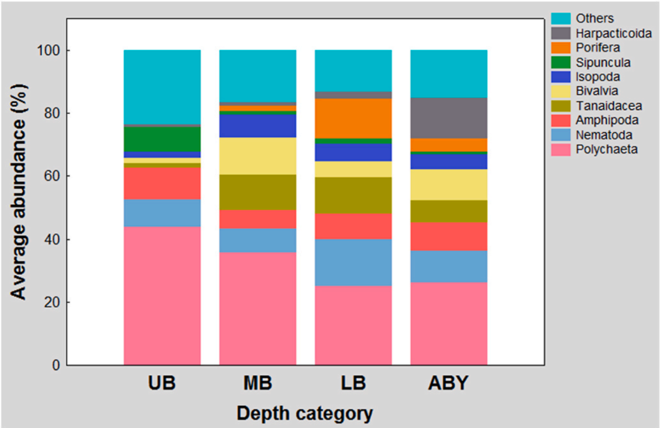

Fig. 3. Percentage of contribution of Polychaeta to relative average abundance of macrofauna by depth category. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

The ANOSIM global R statistic value (0.257), relatively low but greater than anyone of the 999 random permutations done, suggests that there are differences in the community composition of the groups (p <

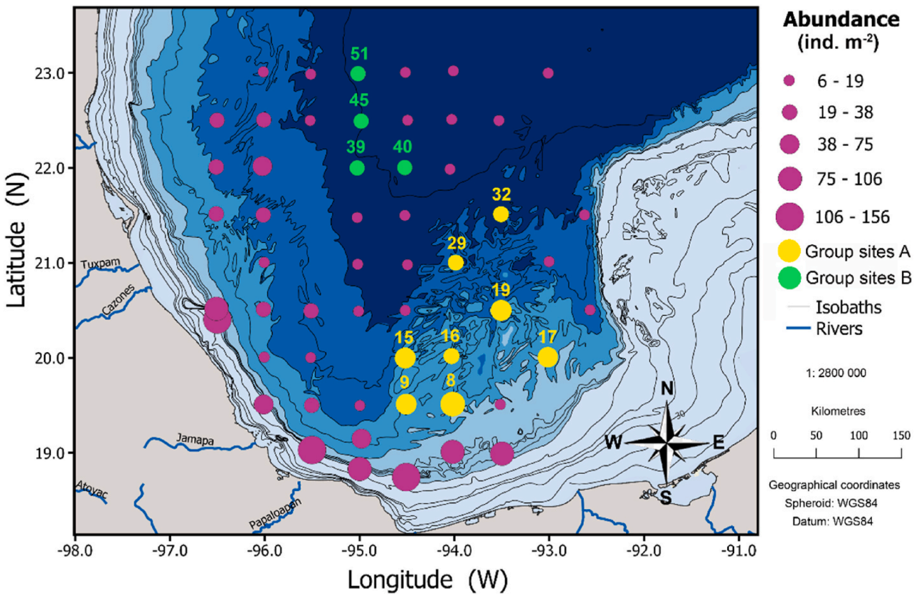

Fig. 4. Geographic distribution of Polychaeta abundance (ind. m^{-2}) in the southwestern Gulf of Mexico.

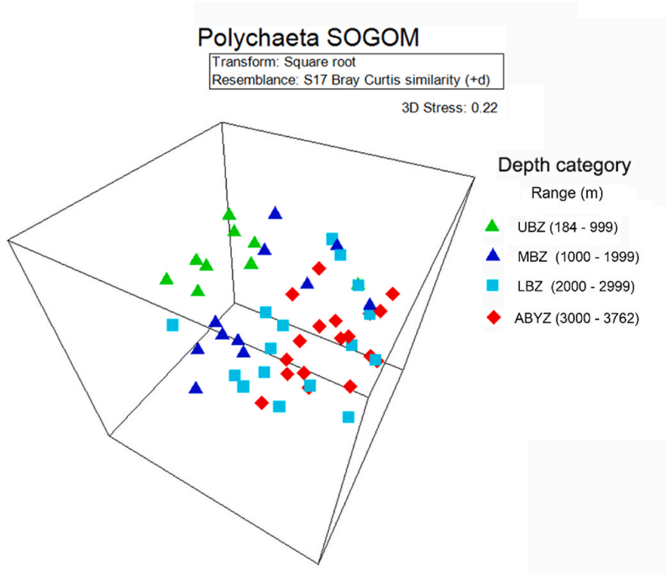

Fig. 5. Non-metric multidimensional scaling results of Polychaeta communities of upper bathyal (green triangles) middle bathyal (blue triangles) lower bathyal (blue squares) and abyssal zones (red squares) based on Bray Curtis similarities and an added dummy variable.

Table 2
ANOSIM results.

One-Way Analysis

Factor Values

Factor: Depth category

1 UBZ
2 MBZ
3 LBZ
4 ABYZ
Global Test

Sample statistic (Global R): 0.257
Significance level of sample statistic: 0.1%
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0
Pairwise Tests

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number ≥ Observed
1, 2	0.232	1.4	167960	999	13
1, 3	0.434	0.1	2042975	999	0
1, 4	0.647	0.1	4686825	999	0
2, 3	0.09	9.2	13037895	999	91
2, 4	0.228	0.2	34597290	999	1
3, 4	0.073	6.1	Very large	999	60

Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

0.001). The specific pairwise test showed the highest R value ($R = 0.647$ $p < 0.001$) when the groups of stations of 185–1000 m depth and those greater than 3000 m were compared. In the comparison within other groups the R statistic value was always under 0.5, particularly lower and not significant within LBZ-ABYZ ($R = 0.073$ $p < 0.061$) and MBZ-LBZ ($R = 0.09$ $p < 0.092$) pairwise comparison (Table 2).

The heat map showed the general composition and structure of the community along depth categories. The genera *Aricidea* Webster, 1879, and *Levinsenia* Mesnil, 1897 registered a high contribution to abundance in all depth categories. *Paradoneis* Hartman, 1965, *Spiophanes* Grube, 1860, *Paramphinome* M. Sars in G. Sars (1872), and *Aphelochaeta* Blake, 1991 were recorded in the four depth categories, but showed the highest contribution to abundance in the deepest zones. *Sigambra* Müller, 1858 was present from UBZ to LBZ with the highest contribution in MBZ. The genera *Ceratocephale* Malmgren, 1867, *Glycera* Lamarck, 1818, *Ophelina* Örsted, 1843 and *Heterospio* Ehlers, 1874 registered an important contribution to abundance from MBZ to ABYZ. In the UBZ, fifteen genera (named as others in Fig. 6 which contributed 10% to the total abundance), besides, *Litocorsa* Pearson, 1970, *Paradiopatra* Ehlers, 1887, *Paraprionospio* Caullery, 1914, and *Prionospio* Malmgren, 1867 registered the highest contribution to abundance in this zone. In the MBZ *Travisia* Johnston, 1840, *Lumbrineris* Blainville, 1828, *Exogone* Örsted, 1845, *Eteone* Savigny, 1822, *Laubieriopsis* Petersen, 2000, *Tachytrypane* *McIntosh, 1876*), and *Notomastus* M. Sars (1851) presented the highest contribution to abundance. On the other hand, *Poecilochaetus* Claparède in Ehlers (1875), *Paraonides* Cerruti, 1909, *Paralacydonia* Fauvel, 1913, *Pseudoscalibregma* Ashworth, 1901, *Trochochaeta* Levinsen, 1884, *Sternaspis* Otto, 1820, *Ophelia* Savigny, 1822, *Ammotrypanella* McIntosh, 1878, *Augeneria* Monro, 1930, *Amphicteis* Grube, 1850, and *Abyssoninoe* Orensanz, 1990 recorded the highest contribution to abundance in the

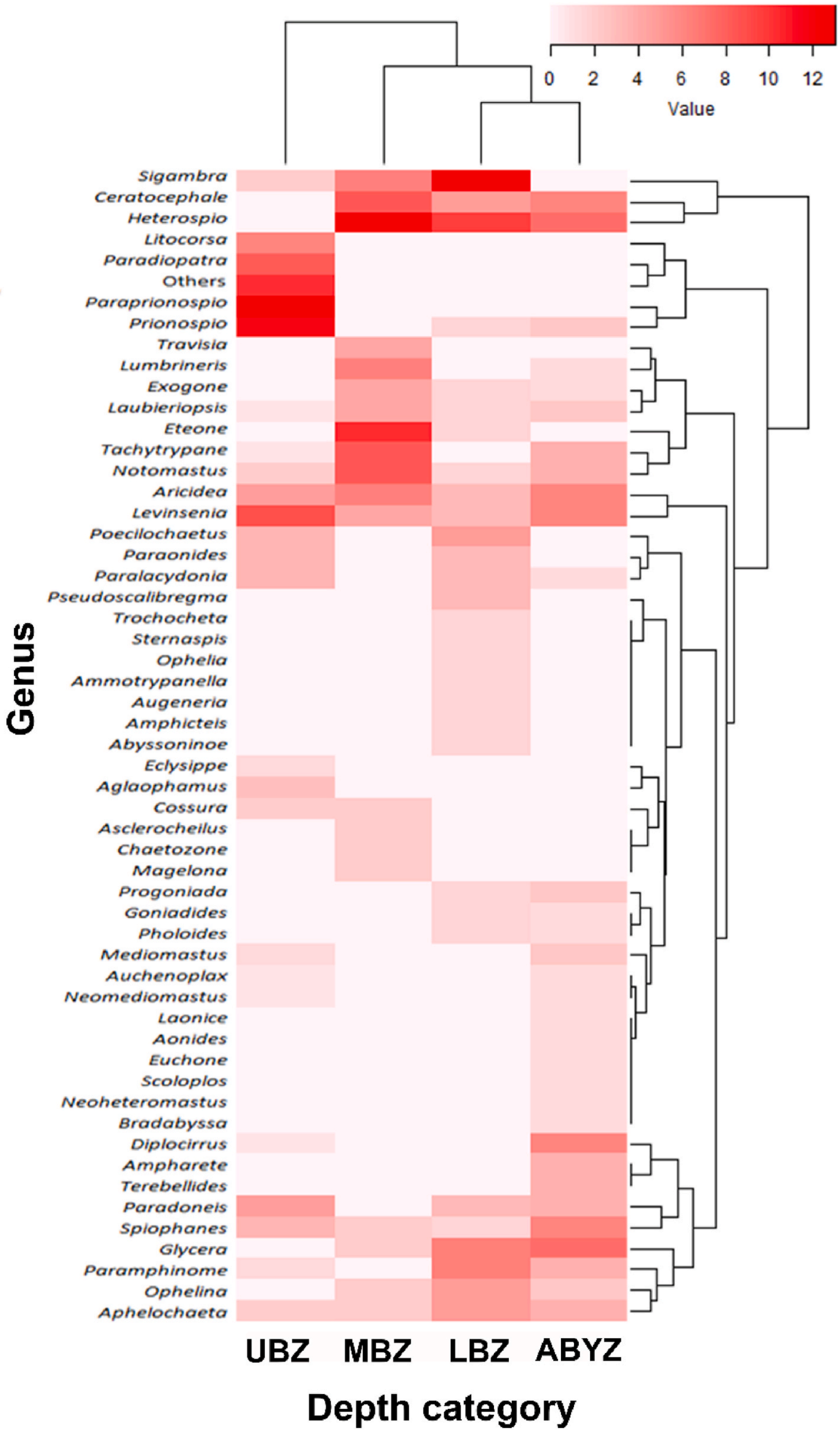

Fig. 6. Heat map of contribution to average abundance by each genus for each depth category. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

LBZ, whereas the first three genera also had a high contribution to abundance in the UBZ. Finally, *Diplocirrus* Haase, 1915, *Ampharete* Malmgren, 1866, and *Terebellides* Sars, 1835 showed a high contribution to abundance in the ABYZ and the genera *Mediomastus* Hartman, 1944, *Auchenoplax(Ehlers, 1887)* , *Neomediomastus* Hartman, 1969, *Laonice* Malmgren, 1867, *Aonides* Claparède, 1864, *Euchone* Malmgren, 1866, *Scoloplos* Blainville, 1828, *Neoheteromastus* Hartman, 1960, and *Bradabyssa* Hartman, 1967 registered a medium contribution (Fig. 6).

Salinity and silt percentage presented high correlation with temperature and clay percentage, respectively, so they were not included in the BEST analysis. The overall analysis of the BEST routine gave a relatively low ρ value (0.35), however, it is greater than any of the 999 values obtained by random permutations. Considering four variables, the highest correlation of genera observed distribution was with: depth, temperature, dissolved oxygen concentration of bottom water and clay percentage in the sediment (Table 3).

In general, the geographic distribution of genus richness showed two regions with highest taxonomic diversity, the saline domes in the Campeche Bay zone and the northwestern zone of the study area (Fig. 7).

Taxonomic diversity estimated through the coverage-based R/E sampling curves (with the three Hill numbers, $q = 0, 1, 2$) showed that the highest values were obtained in the MBZ and LBZ while the UBZ and ABYZ registered the lower ones (Fig. 8 a-c). This pattern is consistent when the comparison is done based on the lower sample coverage registered (0.75 in LBZ) showing an increase in the diversity ($q = 0$ and $q = 1$) from UBZ to LBZ and a clear decrease in the ABYZ. In terms of dominant taxa ($q = 2$) we registered a remarkable increase in diversity from UBZ to MBZ and a less drastic decrease to LBZ and ABYZ (Fig. 8 d-f).

Diversity profile showed four zones with different taxonomic richness ($q = 0$), however, when we analyzed common and dominant ($q = 1$), and particularly dominant taxa ($q = 2$), the zones cluster in two groups, one of highest diverse (MBZ and LBZ) and other of lowest diverse (UBZ and ABYZ) (Fig. 9). This analysis also showed that MBZ and ABYZ presented more evenness than UBZ and LBZ.

Five bioturbation traits were assigned to the genera registered in this study. Four of them were present in all depth categories, but downward conveyors (DC) were only present in the MBZ. Upward conveyors (UC) were more abundant in MBZ and ABYZ compared to UBZ and LBZ. Regarding the others three bioturbation traits, surficial modifiers (S) and upward and downward conveyors (UC/DC), were dominant in the UBZ while biodiffusors (B) contributed with almost 20% to average abundance. When the depth increased, UC/DC practically disappeared, S abundance decreased, and B dominance increased (Fig. 10).

Sixteen feeding guilds were registered in this study. We recorded the highest functional diversity in MBZ (14 feeding guilds), and the lower one in ABYZ (11 feeding guilds). Microphagous was the dominating guild in all depth categories, while the macrophages were more abundant in the two deeper categories. Omnivores practically showed the same abundance in all depth categories. We registered suspension feeders, and surface deposit-feeders in the four depth categories. Both guilds showed a decrease when depth increased, particularly remarkable in the suspension feeders. In general, carnivores increased when depth increased. Detritivores were present only in the three first depth categories, and showed a slight abundance increase related to depth. Subsurface deposit-feeders guild dominated in all depth categories, and showed a relative abundance increase when depth augmented. We registered sessile polychaetes only in MBZ. The motile polychaetes increased, and the discretely motile decreased when depth increased (Fig. 11).

The depth related genera distribution showed distinct patterns. Twenty one genera showed eurybathic distribution. Nine of them (*Levinsenia* Mesnil, 1897, *Notomastus* M. Sars, 1851, *Spiophanes* Grube, 1860, *Aphelochaeta* Blake, 1991, *Cossura* Webster and Benedict, 1887, *Aricidea* Webster, 1879, *Tachytrypane* (McIntosh, 1876), *Laubieriopsis* (Petersen, 2000), and *Sigambra* Müller, 1858) were registered in all depth categories, while six (*Paramphinome* M. Sars in G. Sars, 1872, *Paraonides* Cerruti, 1909, *Prionospio* Malmgren, 1867, *Paradoneis* Hartman, 1965, *Poecilochaetus* Claparède in Ehlers, 1875, and *Paralacydonia* Fauvel, 1913) were found from the UBZ to LBZ and six (*Heterospio* Ehlers, 1874, *Ophelina* *Örsted, 1843*, *Glycera* Lamarck, 1818, *Lumbrineris* Blainville, 1828, *Ceratocephale* Malmgren, 1867, and *Exogone* Örsted, 1845) from the MBZ to ABYZ. Fifteen genera presented a stenobathic distribution. Nine of them (*Mediomastus* Hartman, 1944, *Diplocirrus* Haase, 1915, *Auchenoplax* (*Ehlers, 1887*) , *Neomediomastus* Hartman, 1969, *Paradiopatra* (Ehlers, 1887), *Aglaophamus* Kinberg, 1866, *Litocorsa* Pearson, 1970, *Paraprionospio* Caullery, 1914, and *Eclysippe* Eliason, 1955) were found in the shallower zone while other six (*Pholoides* Pruvot, 1895, *Terebellides* Sars, 1835, *Ampharete* Malmgren, 1866, *Progoniada* Hartman, 1965, *Goniadides* Hartmann-Schröder, 1960, and *Eteone* Savigny, 1822) in intermediate depths (Fig. 12). Thirty-three of the genera collected, presented a single record, 15 were observed in UBZ, 6 in MBZ, 8 in LBZ, and 4 in ABYZ (Fig. 13).

4. Discussion

Benthic macrofauna communities in general, and Polychaeta in particular, are poorly understood due to the difficulty and high cost of conducting deep sea research (Reuscher and Shirley, 2017). It is known that in the deep sea, diversity is high, abundances are low, dominance is not common and, often, only one individual per species is recorded in each locality sampled (Danovaro et al., 2014; Gage, 2001; Hargrave and Thiel, 1983). The most abundant families (Spionidae and Paraonidae) and most diverse (Spionidae, Capitellidae, Paraonidae, Ampharetidae, Lumbrineridae, and Opheliidae) registered in this study are consistent with those reported in previous deep sea studies in other oceans (Cosson-Sarradin et al., 1998; Glover et al., 2001; Paterson et al., 1998) and in the north (Carvalho et al., 2013; Fauchald and Jumars, 1979), and southwestern of GM (Pérez-Mendoza et al., 2003). The decrease of the polychaetes contribution to macrofauna average abundance when depth increases is in part explained by the relative contribution increment registered in other groups, *e.g.*, the suborder Asellota (Isopoda, Arthropoda) (Wilson, 2008) , ; the class Hexactinellida (Porifera) (Dohrmann et al., 2008; Krautter et al., 2001); the order Harpacticoida (Copepoda, Arthropoda) (Brandt et al., 2018) the suborder Tanaidacea (Peracarida, Arthropoda) (Larsen, 2005; Wilson, 1987) and the class Bivalvia (Mollusca) (Shantharam and Baco, 2020), which have been reported as diverse and abundant taxa within macrobenthic communities in deep waters. Nonetheless, the polychaetes contribution to macrofaunal abundance in ABYZ registered in this study is similar to that reported in the Atlantic abyssal zone (25.7%) (Brandt et al., 2018).

The subsample size (0.08 m2), lower than the standard sample surface commonly used for deep sea, and mesh sieve (500 μm) used in this study affected the sampling effort and may have influenced the registered abundance values. We recorded polychaete abundance values (6–140 ind. m^{-2}) lower than those reported for the northern Gulf of Mexico. For example, Reuscher and Shirley (2017) reported 250–2800 ind. m^{-2}, Carvalho et al. (2013) recorded 300–3800 ind. m^{-2}, Qu et al. (2016, 2017) registered 270–3500 ind. m^{-2} and 1416 1707 ind. m^{-2} on average, respectively. It is important to highlight that those previous

Table 3
BIOENV results.

BEST Biota and/or Environment matching		Best results		
Parameters	Variables	No. Vars	Corr.	Selections
Rank correlation method: Spearman	1 Depth (m)	4	0.359	1-3,6
Method: BIOENV	2 Temperature (°C)	3	0.351	2,3,6
Maximum number of variables: 4	3 Dissolved oxygen (mL^{-1})	3	0.347	1,2,6
Resemblance:	4% Carbonates	4	0.346	2-4,6
Analyze between: Samples	5% Organic matter	3	0.342	1–3
Resemblance measure:	6% Clay	3	0.340	1,3,6
D1 Euclidean distance	7% Sand	4	0.338	2,3,5,6
		2	0.337	1,2
		4	0.336	1-3,5
		2	0.336	1,3
Global Test				
Sample statistic (Rho): 0.359				
Significance level of sample statistic: 0.1%				
Number of permutations: 999 (Random sample)				
Number of permuted statistics greater than or equal to Rho: 0				

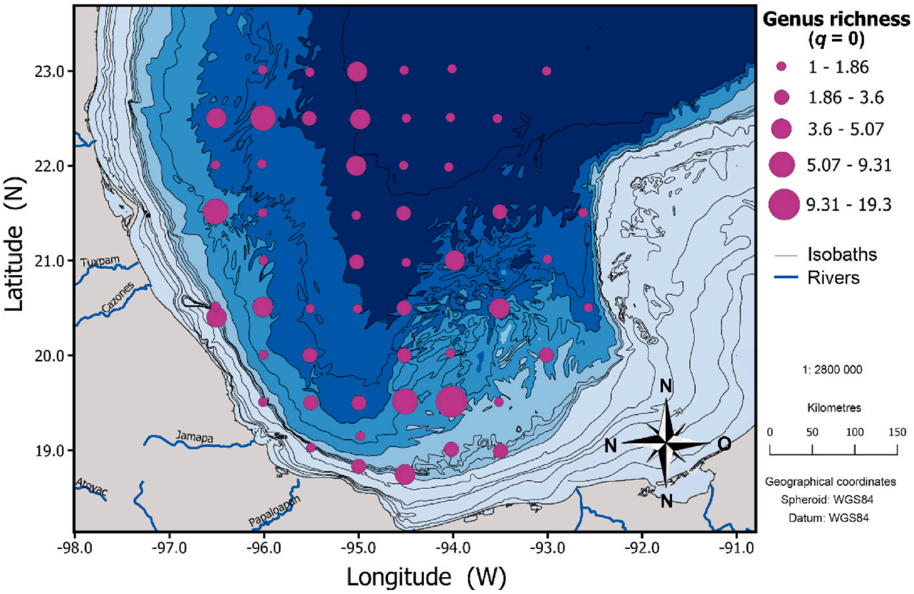

Fig. 7. Geographic distribution of Polychaeta genus richness ($q = 0$) in the southwestern Gulf of Mexico.

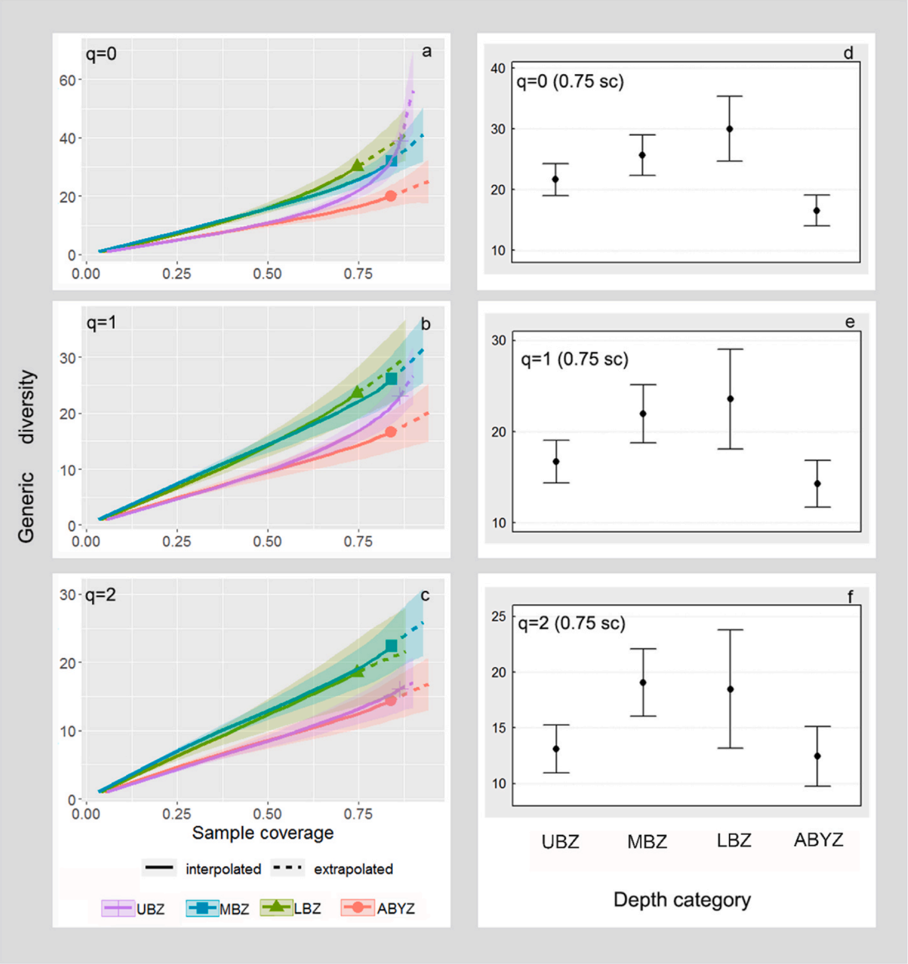

Fig. 8. a-f. Coverage-based R/E (rarefaction and extrapolation) sampling curves and comparison between depth categories at 0.75 sample coverage for three Hill numbers ($q = 0$, 1, and 2). Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

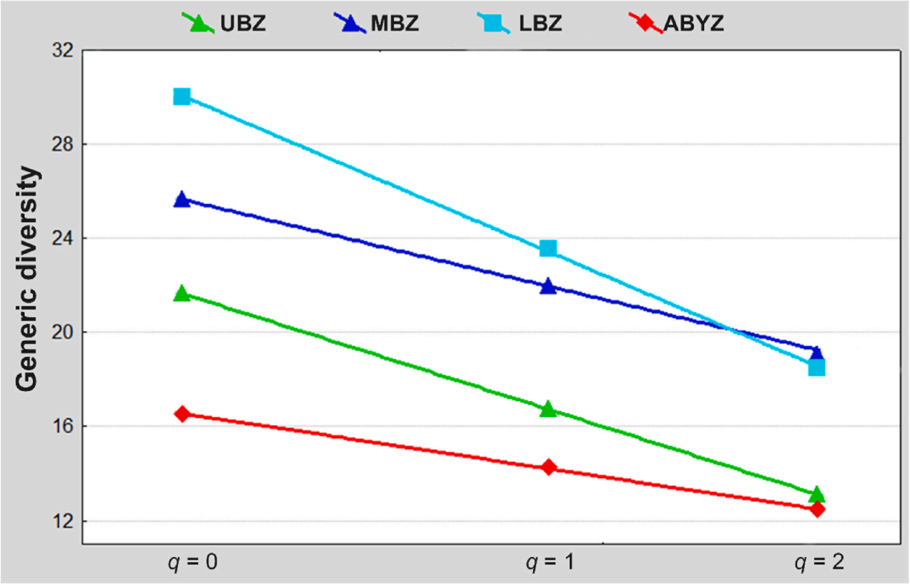

Fig. 9. Diversity profile between depth categories at 0.75 sample coverage. Hill numbers $q = 0$, 1, and 2. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

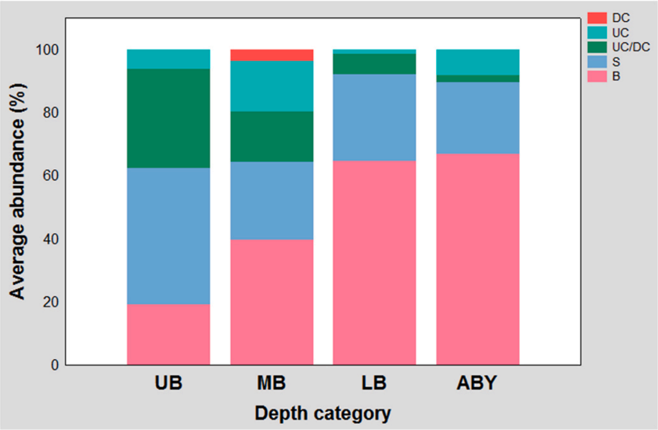

Fig. 10. Percentage contribution of bioturbation traits to average abundance. Downward conveyors (DC); upward conveyors (UC); upward and downward conveyors (UC/DC); surficial modifiers (S) and biodiffusors (B). Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

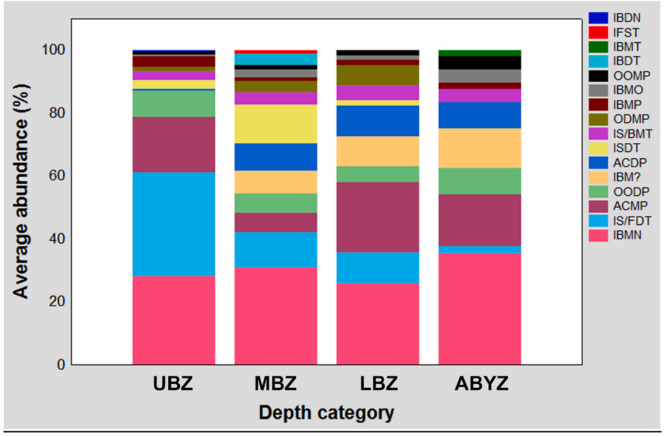

Fig. 11. Percentage contribution of feeding guilds to average abundance. The letters meaning in the acronym are: 1) I = microphagous; A = macrophagous, and O = omnivore. 2) B = subsurface deposit feeder; S = surface deposit feeder; F = suspension feeder; O = omnivore, and C = carnivore/scavenger. 3) M = motile; D = discretely motile, and S = sessile. 4) N = nonmuscular eversible pharynx; T = tentacle/palps; P = muscular eversible pharynx, and O = other. Therefore, ISMP = microphagous, surface deposit feeder, motile, and no muscular proboscis. Upper bathyal zone (UBZ); middle bathyal zone (MBZ); low bathyal zone (LBZ) and abyssal zone (ABYZ).

studies were carried out using a smaller mesh size (300 μm) than the present research, which prevents a direct comparison. Additionally, it must be noted that we found many fragments and damaged specimens impossible to identify, which could increase the abundance values (at least four times), but still the numbers are remarkably lower than the abundance values registered in the North of Gulf of Mexico. However, Pérez-Mendoza et al. (2003) reported abundance values similar to ours (6–260 ind. m^{-2}) in the southern Gulf of Mexico using a 250 μm mesh. This may suggest differences of Polychaeta abundance for the North and South of the Gulf of Mexico perhaps influenced by environmental factors among which the Mississippi river runoff could be one of the most important. Blomberg and Montagna (2014) mentioned that productivity in the GM is related to runoff from land. It is important to highlight that the low sampling effort could limit the use of the abundance data as baseline and should be taken with caution when analyzing potential oil spill impacts. However, the data recorded is useful and valuable of the polychaete assemblages of southwestern GM and can be used as a basis for further studies.

We observed a depth-related abundance pattern. In general, the highest values were recorded in the UBZ and the lowest ones in the ABYZ. This is similar to the global observed depth-related pattern (Rex et al., 2006), also found in the GM (Carvalho et al., 2013; Qu et al., 2017). However, some authors report variations in this depth-related pattern in GM, *e.g.*, an inverted parabola shape pattern has been reported (Pérez-Mendoza et al., 2003) as well as an inconsistency in the expected abundance decreasing trend as depth increases between 325 and 1500 m and a subsequent abundance strong decrease beyond this depth (Reuscher and Shirley, 2017). The abundance depth-related pattern we registered has been explained elsewhere by the decrease in organic carbon (CO) flux (Rex et al., 2006) as depth and distance from the coastline augment. Indeed, we registered a consistent decrease in sediment organic matter concentration as depth increased. This

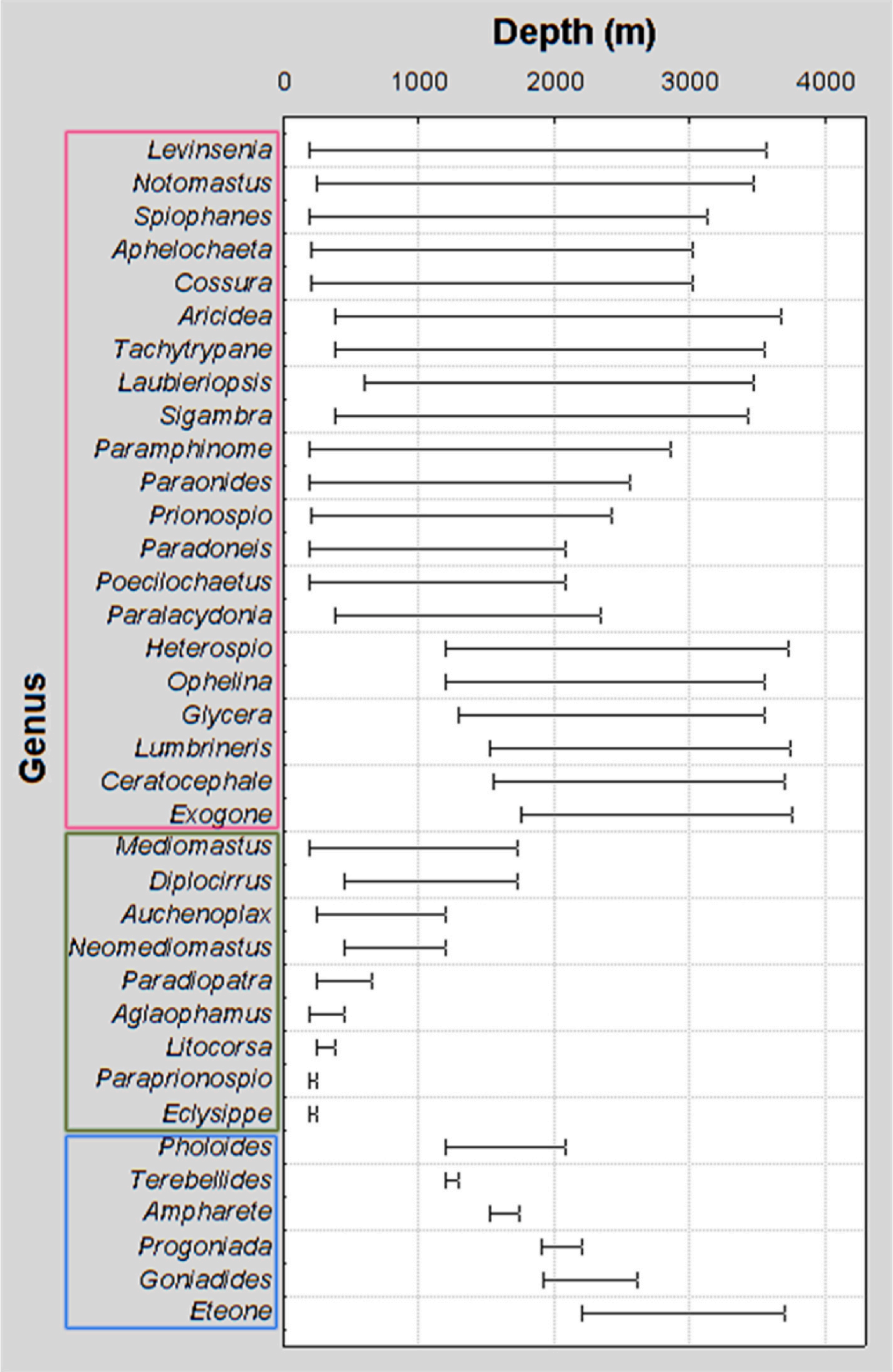

Fig. 12. Bathymetric distribution on Polychaeta genera with at least two records. Eurybathic taxa (red box); stenobathic taxa (green, and blue boxes).

behavior was previously reported in the southwestern GM deep sea region for sediment CO distribution (Escobar-Briones and García-Villalobos, 2009) with the highest values recorded in relatively shallow areas close to the coast that also coincides with the general pattern of abundance registered. We found relatively high abundances in eight coastal sites located along the southern margin of Campeche Bay that receive CO load from the Grijalva Usumacinta river system, the most important one contributing freshwater and continental sediments to the GM (Toledo-Ocampo, 2005) only after the Mississippi river. Furthermore, these sites are in an area where there are a high number of hydrocarbon natural seeps that support primary chemosynthetic producer communities (Sahling et al., 2016) and do not depend primarily on the input of CO from surficial waters. In this type of environment, high abundance values of polychaetes and bivalves have been previously reported (MacDonald et al., 1989). Besides, 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 subsequently the export of CO to the GM bottom. These factors together can explain the high abundance values observed in the southern region of the study area. Some deeper sites, like 39, 40, 45, and 51 also presented relatively high abundances which can also be related to CO concentrations. These sites are close to the continental rise where a relative high sedimentation rate was documented compared to continental slope and abyssal plain (Díaz-Asencio et al., 2019). This could result in an accumulation of CO

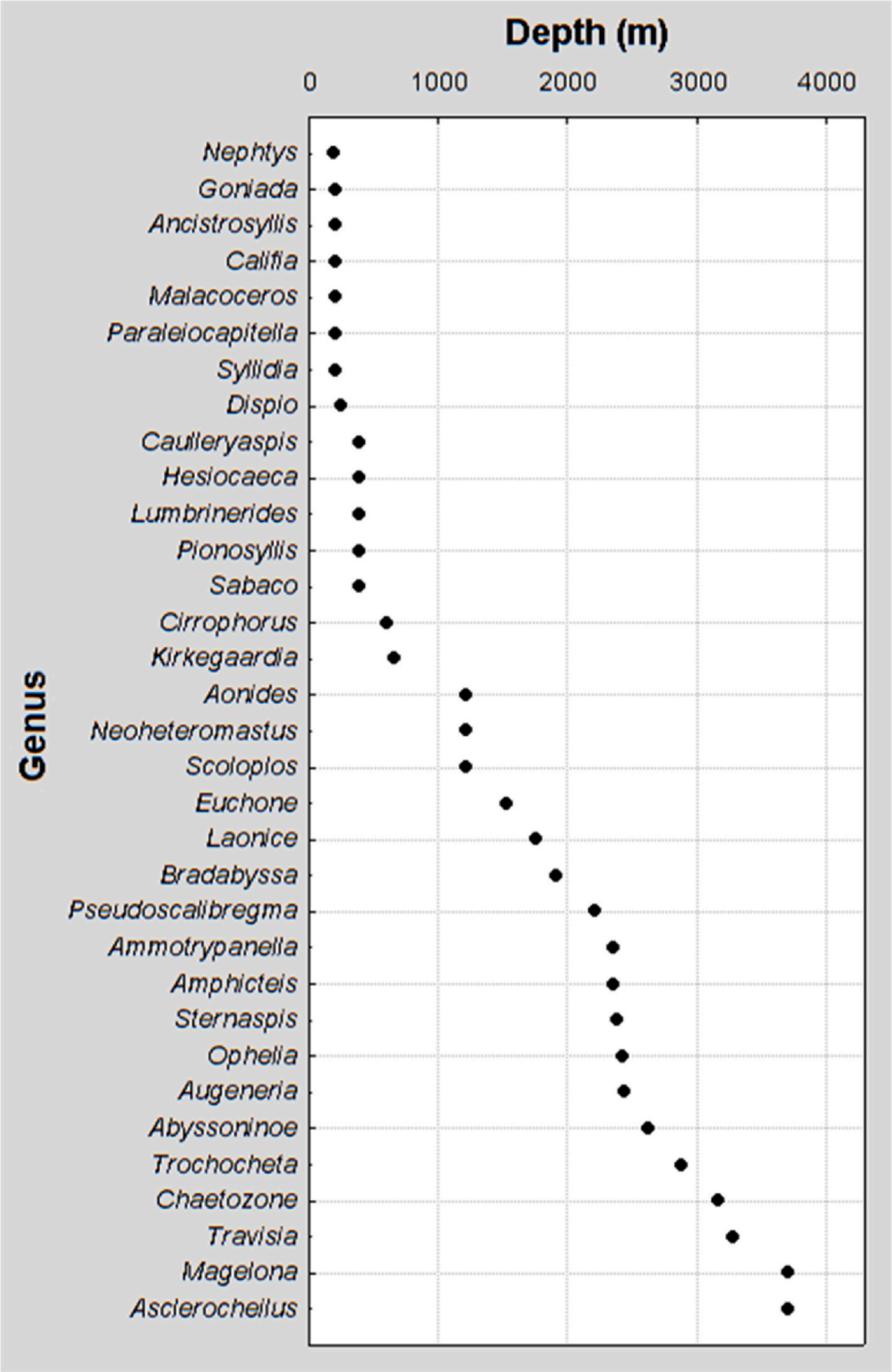

Fig. 13. Bathymetric distribution on Polychaeta genera with a single record.

exported from the surface layers that could promote a higher abundance in this area.

The gradual change in the composition and structure, in terms of relative abundances of the polychaete communities related to depth shown by the NMDS analysis, is confirmed by the ANOSIM pairwise comparison results. The upper bathyal zone and the abyssal zone are separated ($R = 0.646$ $p < 0.001$) while the R values between adjacent bathymetric categories do not show a clear separation. These results are consistent with the general macrofauna and polychaete distribution patterns reported in other studies (Wei et al., 2010b; Reuscher and Shirley, 2017) in the deep sea of GM. According to Brown and Thatje (2014), hydrostatic pressure (depth) and temperature constitute a physiological bottleneck that generates a bathymetric zonation in the distribution of species and prevents that most of the shallow species could have a wide bathymetric distribution. The genera belonging to Spionidae and Paraonidae were highlighted as important taxa in the bathymetric zonation by the heat map analysis. The family Spionidae, in particular, was previously reported to be well represented in the deep waters (Langeneck et al., 2017), principally the genera *Prionospio* Malmgren, 1867, and *Spiophanes* Grube, 1860 that are two of the three more common spionid genera in deep sea (Blake, 1983). We registered *Spiophanes* Grube, 1860 in all depth categories with relative high abundance, but *Paraprionospio* Caullery, 1914, and *Prionospio* Malmgren, 1867 were only abundant in UBZ and absent in the deepest zone.

The family Paraonidae is also known to be widely represented in deep waters (Langeneck et al., 2017; Strelzov, 1979), which was confirmed in our study with the genera *Levinsenia* Mesnil, 1897, and *Aricidea* Webster, 1879 registered in all depth categories with high abundance, and the genus *Paradoneis* Hartman, 1965 absent in MBZ but present in the other depth categories with relative high abundance. *Heterospio* Ehlers, 1874, that contributes greatly to abundance from MBZ to ABYZ, has been reported as the dominant genus in the bathyal Ionian Sea region (Langeneck et al., 2017). The genus *Sigambra* Müller, 1858 was not very abundant, but it had a considerable contribution to the general abundance in intermediate depths with an important occurrence in the three bathyal depth categories. Finally, *Notomastus* M. Sars (1851), the fifth most important genus in terms of occurrence, was registered in all depth categories with the highest contribution to abundance in the MBZ and ABYZ, which is consistent with the report of Capitellidae as an important family in deep waters (Qu et al., 2016).

The environmental factors that presented the highest correlations with the faunal distribution have been reported as structuring elements of the deep sea benthic communities, namely depth and temperature (Brown and Thatje, 2014), oxygen concentration (Levin and Gage, 1998), and sediment granulometry (Etter and Grassle, 1992). In the GM deep sea, depth (and its associated variables) was also reported as an important structuring factor of polychaete communities (Carvalho et al., 2013; Qu et al., 2016; Reuscher and Shirley, 2014, 2017). Carvalho et al. (2013) also pointed out the contribution of CO as an explanatory variable of the polychaetes distribution patterns. However, despite the evidence of the correlation between the CO and benthic communities' distribution (Morse and Beazley, 2008; Wei et al., 2010b), our BEST analysis results did not include the OM within the environmental factors with the highest correlation. However, when OM is included (in the seventh best result), the correlation value is very close to the highest value obtained (Table 3).

The highest diversity observed in the Campeche Bay in this study could be explained in part by the relative high habitat heterogeneity due to presence of important hydrocarbons seepages. According to Cordes et al. (2010, 2009) subsurface hydrocarbons seeps play an important role in increasing habitat heterogeneity in the deep sea. This results in a variety of macrofaunal and meiofaunal communities that respond to changes in structural complexity habitat, geochemistry, nutrient sources, and interspecific interactions (Cordes et al., 2010) increasing local alpha and beta diversity (Jones et al., 2014). The region of the Campeche Knolls shows evidence of abundant natural hydrocarbon seeps with widespread occurrence of asphalt deposits. Seepage of oil and gas bubbles co-occurs next to and through them (Sahling et al., 2016). These conditions also implicate chemosynthetic primary productivity with less dependence of surficial layer export CO. In this region, we registered the families Paraonidae, Amphinomidae, Orbiniidae, Ampharetidae, and Capitellidae that are usually associated with cold-seeps (Levin, 2005). These families were present in seven of eight sites with relative high taxonomic richness (between one and five families per site). Moreover, this region presents important CO fluxes by the Grijalva Usumacinta System Rivers and by the presence of a quasi-permanent cyclonic eddy. This increases productivity within the system and allows to sustain a greater diversity (Carrara and Vázquez, 2010; Woolley et al., 2016). Another region with relative high diversity in the northwestern zone of study area has been indicated as an area with hydrocarbon natural seeps (Williams et al., 2006; Gracia personal observations) whose habitat conditions could be like those of the Campeche Bay.

The bathymetric diversity analysis showed the lowest taxonomic richness in the upper bathyal and abyssal zones while the highest one was in the middle and low bathyal zones for any order included in the analysis ($q = 0, 1, 2$). This matches with the classic unimodal pattern described for deep sea including the GM with the lowest diversity in the upper bathyal and the abyssal zones and the highest diversity in the intermediate depths (Etter and Grassle, 1992; Rex, 1981; Rex et al., 2006). This pattern has been explained by productivity and disturbance (Cosson-Sarradin et al., 1998; Paterson and Lambshead, 1995; Rex et al., 2005) among others environmental gradients. Also, it was attributed to the elevated speciation rate due to high biological variability promoted by the physiological bottleneck at bathyal depths because of the high hydrostatic pressure and low temperature (Brown and Thatje, 2014). However, this pattern is not always fulfilled (Stuart et al., 2003). For example, Qu et al. (2017) report for the north of the GM that the highest diversity of polychaetes was found at 900 m depth (UBZ). These exceptions can be explained by horizontal environmental characteristics such as oxygen minimum zones (see Levin et al., 2001; Stuart et al., 2003) that modify the general bathymetric trend. In this study we registered the lowest oxygen concentration in the UBZ and the lowest organic matter concentration in the ABYZ, both environmental factors could be affecting the diversity values observed.

In general, we registered a decrease in functional diversity with increasing depth in both evaluated traits (bioturbation and feeding guilds). In the case of bioturbation traits, the biodiffusors dominated the deepest zones. This trait includes organisms with behavior that usually result in a constant and random local sediment biomixing over short distances resulting in transport of particles like molecular diffusion in the sense of Kristensen et al. (2012). On the other hand, the activity of DC, UC and DC/UC organisms that occur mainly in UBZ and MBZ, implicates greater removal of particles including burial of surface sediments with labile organic matter and/or associated pollutants in addition to the formation of mounds on the surface of the sediment (Kristensen et al., 2012). In this way, the bioturbation effect decreases with increasing depth, which is enhanced by macrofaunal abundance decrease and reduction of fauna size (Rex et al., 2006; Wei et al., 2010a). On the other hand, the permanence of biogenic structures in the ocean floor lasts longer in deep sea than in shallow areas due to the lower frequency of disturbance processes.

About feeding guilds, we recorded a sub-surface deposit-feeders dominance in the deepest zones like the functional diversity pattern based on feeding guilds reported by Carvalho et al., (2013). It is known that in the deep sea the functional structure is very similar, and it is dominated by deposit feeders in macrobenthos in general, and particularly in polychaetes (Glover et al., 2001; Langeneck et al., 2017, 2019). We also observed an increase of carnivores with depth increase. Our results of carnivore's abundance contribution (near 15%) to total abundance in MBZ agree with that reported by Langeneck et al. (2017) in the western Ionian Sea. However, our findings are not coincident to indicate that surface deposit feeders were the largest contributor traits in MBZ. Instead, we observed that subsurface deposit feeders showed the highest contribution. Also, we registered omnivores in all depth categories, with practically the same relative abundance, while Langeneck et al. (2019) observed this trait from 600 m to 2400 m depth. However, they registered a progressive relative abundance decrease when depth increased. Another important difference is that they registered the lowest relative abundance of suspension feeders in the shallowest zones, while we registered the highest relative abundance in shallow areas.

This first approximation to understand the polychaete communities showed important information and highlighted the need to develop further studies in the Mexican deep sea of the Gulf of Mexico.

5. Conclusions

This study constitutes the most important effort to date to understand the polychaete communities in the Mexican deep waters of the southern Gulf of Mexico. The Polychaeta contribution to total macrofaunal abundance showed a decrease related to depth increase within a range of 25 %–44%. The sites of highest abundance values were located near shore in the southern region, and in the northwestern region of the study area. Among the 33 families registered, Spionidae, Paraonidae, Pilargidae, Capitellidae and Longosomatidae were the most abundant. Besides, Spionidae, Capitellidae and Paraonidae were the more diverse families. Sixty-nine genera were registered. The most abundant were

Levinsenia Mesnil, 1897, *Prionospio* Malmgren, 1867, *Paraprionospio* Caullery, 1914, *Heterospio* Ehlers, 1874, and *Aricidea* Webster, 1879, while the most frequent were *Heterospio* Ehlers, 1874, *Levinsenia* Mesnil, 189, *Aricidea* Webster, 1879, *Sigambra* Müller, 1858, and *Notomastus* M. Sars (1851). This study showed a bathymetric-related change in composition and structure of the polychaetes community. Temperature, bottom water dissolved oxygen concentration and sediment granulometry were identified as the main drivers of community structure. The highest taxonomic diversity was registered at intermediate depths and functional diversity was found to decrease with increasing depth.

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.

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Discusión

Análisis ambiental

Las diferentes zonas del área de estudio definidas de acuerdo a la profundidad presentaron características distintivas. La UBZ se caracterizó por presentar importantes variaciones de oxígeno disuelto, salinidad y temperatura, alto contenido de MO y limo, bajo contenido de carbonato y arcilla en sedimentos, además de altos valores de hidrocarburos aromáticos. Mientras que las regiones LBZ y AZ se distinguieron por registrar valores altos de oxígeno disuelto (OD) y estabilidad en los valores de salinidad y temperatura del agua de fondo. También, bajos valores de materia orgánica y limo, altos valores de carbonato y arcilla e hidrocarburos aromáticos relativamente más bajos en los sedimentos (Quintanar-Retama et al., 2022; 2023). Todos estos factores ambientales han sido relacionados con la distribución de las comunidades bentónicas de aguas profundas. La temperatura y la presión hidrostática han sido documentadas como factores promotores de la zonificación faunística debido a que establecen un cuello de botella fisiológico que limita la distribuciónbatimétrica de especies de aguas someras (Allen, 2008; Brown y Thatje, 2014). Se han documentado adaptaciones como el aumento de la concentración mitocondrial y la adopción de formas de enzimas más eficientes a bajas temperaturas (Clarke, 1998). La importancia de la temperatura como estructurador de las comunidades bentónicas en aguas profundas se puede observar en el patrón de distribución registrado en regiones como la Antártida donde el gradiente batimétrico no implica un gradiente de temperatura significativo y es muy común registrar especies euribáticas (Brey et al., 1996; Brandt et al.,2007) de tal forma que no suele registrarse la típica zonificación de regiones templadas o tropicales. También, el oxígeno (Levin y Sibuet, 2012) y la disponibilidad de materia orgánica (Cosson et al., 1997; Mamouridis et al., 2011; Bernardino et al., 2016; Brandt et al., 2018; Guggolz et al., 2018) han sido documentados como factores que inciden en la distribución de las comunidades bentónicas de aguas profundas.

Los valores de salinidad y temperatura que registramos en profundidades mayores a 1000 m concuerdan con los de la masa de agua reportada en el GoM con características similares a las Aguas Profundas del Atlántico Norte. Esta masa de agua se caracteriza por presentar valores de salinidad y temperatura cercanos a 35 UPS y 4 °C, respectivamente. Además, valores de oxígeno disuelto superiores a los registrados en capas adyacentes menos profundas (Rivas et al., 2005; Díaz-Asencio et al., 2019).

Los contenidos de carbonatos y de materia orgánica mostraron un patrón relacionado con el aumento de la profundidad consistente en un aumento del primero y una disminución del segundo. Estos patrones concuerdan con lo observado previamente en la región (Escobar-Briones y García-Villalobos, 2009). En el suroeste del GoM predominan los sedimentos de origen terrígeno (Balsam y Beeson, 2003; Díaz-Asencio et al., 2019) con un importante componente de sedimentos biogénicos carbonatados que aumentan su concentración con la profundidad y la distancia a la línea de costa (Balsam y Beeson, 2003). De acuerdo con Balsam y Beeson, (2003) en el GoM se registraron valores de contenido de carbonato de hasta 50% en la zona abisal y 75% en la zona cercana a la plataforma de Yucatán. Nosotros registramos valores de hasta un 24% en la región abisal. Además, esta tendencia observada coincide con un patrón inverso reportado para sedimentos terrígenos (Díaz-Asencio et al., 2019) con los valores más altos cerca de la línea de costa y la concentración más baja en la región abisal. La concentración de materia orgánica en mares marginales como el GoM tiende a disminuir a medida que aumenta la profundidad y la distancia a la costa (Gage y Tyler, 1991; Ramirez-Llodra et al., 2010). Esta tendencia ha sido documentada en el GoM (Morse y Beazley, 2008; Escobar-Briones y García-Villalobos, 2009) y es concordante con nuestros resultados. En cuanto a la granulometría de los sedimentos, observamos patrones batimétricos caracterizados por una disminución de la concentración de limo y un aumento de la concentración de arcilla al incrementarse la profundidad.

Con respecto a los hidrocarburos, las altas concentraciones de PAH en la UBZ de la zona sur se pueden explicar por la presencia de numerosas filtraciones de petróleo encontradas en esta zona, las actividades de las plataformas petrolíferas y la influencia de varios ríos que introducen contaminantes al medio marino (Gracia et al., 2014). El rango de concentración de PAH (56-125 µg kg-1, y 59-158 µg kg-1 para SOGOM 3 y SOGOM 4, respectivamente) está dentro del reportado para el Sur del Golfo de México y (aunque dentro de los valores más bajos) dentro del intervalo registrado en el área de las plataformas petroleras adyacente (16–953 µg kg-1) ubicada en la plataforma continental (Gracia et al., 2016a, 2016b). Es conveniente mencionar que se han registrado valores similares (84 µg kg-1- 158 µg kg- 1) en sedimentos de la zona profunda del norte del GoM (Adhikari et al., 2016). Los valores de hidrocarburos alifáticos permanecieron relativamente constantes a lo largo del intervalo de profundidad analizado con algunos picos de mayor concentración en sitios con profundidades superiores a 2000 m lo cual podría deberse a las abundantes filtraciones de hidrocarburos reportadas en la región (Sahling et al., 2016).

Descripción de la fauna

La composición taxonómica, a nivel de grandes grupos, que registramos de las comunidades de macrofauna incluyó doce filos típicos de mar profundo (Grassle, 1991). Dentro de los 25 taxones registrados, los cinco más abundantes fueron Polychaeta, Amphipoda, Tanaidacea, Bivalvia y Nematoda. Entre estos, la dominancia de poliquetos (43% en SOGOM 3 y 46% en SOGOM4) es común en los estudios en aguas profundas (Hessler y Sanders, 1967; Hessler y Jumars, 1974; Alongi, 1992; Brandt y Schnack, 1999; Paterson et al., 2009; Bernardino et al., 2016; Brandt et al., 2018, 2019, Hernández-Ávila et al., 2021). En el análisis a nivel taxonómico de familia también registramos taxones típicos de mar profundo. Las familias de poliquetos más abundantes fueron Spionidae, Paraonidae, Cirratulidae y Capitellidae, todas ellas documentadas como taxones abundantes y ampliamente distribuidos en las profundidades marinas de otras regiones (Cosson-Sarradin et al., 1998; Glover et al., 2001; Paterson et al., 1998; Strelzov, 1979), en el norte del GoM (Carvalho et al., 2013; Reuscher & Shirley, 2017) y, dentro del área de estudio (Pérez-Mendoza et al., 2003). En el caso de los peracáridos, registramos a Amphipoda como el orden más abundante lo cual concuerda con lo reportado en otros mares (Brandt et al., 2007; Brökeland et al., 2007; Di Franco et al., 2021) y en el GoM (Demopoulos et al., 2014; Hernández-Ávila et al., 2021). Sin embargo, esto no siempre sucede. Isopoda también suele registrarse como el orden dominante (Brandt et al., 2005; Golovan et al., 2013) y los anfípodos se han llegado a registrar entre los órdenes menos abundantes (Brandt et al., 2005). Según Golovan et al., (2013), la proporción de cada orden de peracáridos en aguas profundas varía considerablemente según la profundidad de muestreo y la ubicación geográfica. Además, como se señaló en los capítulos anteriores, se debe considerar que el tipo de dispositivo utilizado para realizar el muestreo puede ser la causa de un sesgo que dé como resultado una representación dominante de un orden. En estudios en los que se utilizó un trineo epibentónico, los peracáridos suelen ser el taxón dominante dentro de la macrofauna (Brandt et al., 2005) y los mísidos e isópodos los órdenes más abundantes dentro de ella (Brandt et al., 2005; Almeida et al., 2017). En nuestro estudio, el uso del box corer pudo haber dificultado la captura de grupos como los mísidos o algunos isópodos como los pertenecientes a la familia

Munopsidae que tienen alta capacidad de natación (Brandt et al., 2007). Hernández-Ávila et al., (2021) reportaron la misma composición de los órdenes Peracarida registrada en este estudio (Amphipoda, Tanaidacea, Isopoda y Cumacea) referente a la contribución a la abundancia total en un estudio realizado con el mismo tipo de nucleador y el mismo tamaño de luz de malla que usamos, además de realizarlo en la región norte del área de estudio.

En el caso de los aplacóforos, dominó Caudofoveata (86% de la abundancia total) sobre los Solenogastres. Estos, no se lograron identificar a nivel de familia debido a su pobre estado de conservación. Caudofoveata se encuentran principalmente en sedimentos blandos, mientras que Solenogastres son epibentónicos (estilo de vida parcialmente epizoico en sus presas cnidarias) y algunos infaunales (Todt et al., 2008). De tal forma que, como en los peracáridos, el dispositivo utilizado para recolectar las muestras podría explicar parcialmente nuestros resultados ya que es efectivo para muestrear la infauna pero poco eficiente para recolectar organismos epibentónicos con movilidad. Por el contrario, estudios en los que se utilizó un trineo epibentónico tienden a registrar a Solenogastres mejor representada que Caudofoveata (por ejemplo, Linse y Schwabe, 2018). Prochaetodermatidae dominó dentro de Caudofoveata. Este taxón, que representó el 48% de la abundancia total, ha sido documentado como típico de aguas profundas, registrado a lo largo del talud continental y en ocasiones en alta abundancia (Corrêa et al., 2018), de tal forma que puede ser el segundo taxón más abundante dentro de los moluscos (Washburn et al., 2017).

La abundancia disminuyó al aumentar la profundidad. Este patrón lo registramos con los grandes grupos taxonómicos de la macrofauna, con las familias de poliquetos y con las familias de peracáridos y, aunque fue menos claro, también se presentó en las familias de aplacóforos. Dicha tendencia ha sido ampliamente documentada en el mar profundo (Hessler y Sanders, 1967; Gage y Tyler, 1991; Wei et al., 2010a, 2012a; Baldrighi et al., 2014; Bernardino et al., 2016) y se ha relacionado con los cambios en la disponibilidad de materia orgánica que se observa con el aumento de la profundidad (Morse y Beazley, 2008) y la distancia a la costa (Escobar-Briones y García-Villalobos, 2009). También se observó una disminución del contenido de MO en sedimentos relacionada con el aumento de la profundidad. Algunos autores (Pérez-Mendoza et al., 2003; Hughes y Gage, 2004) han reportado inconsistencias en este patrón batimétrico relacionadas con cambios locales en las variables ambientales promotoras de la abundancia de infauna. En este sentido, también registramos sitios que se desviaron del patrón general de abundancia relacionado con la profundidad. Estas localidades se ubicaron en áreas con altas tasas de sedimentación (levantamiento continental, cañón de Coatzacoalcos) que promueven la acumulación de MO, favoreciendo una alta abundancia (Vetter y Dayton, 1998; Escobar-Briones et al., 2008).

Geográficamente, los sitios de mayor abundancia se ubicaron cerca de la línea de costa en la región sur y en la zona de domos salinos de la Bahía de Campeche además de la región noroeste del área de estudio. Por otro lado, los valores más bajos se registraron en la llanura abisal ubicada en la región noreste del área de estudio. Estos resultados fueron similares para los grandes grupos taxonómicos de la macrofauna y para las familias de poliquetos y peracáridos. Aunque con menos sitios registrados, también los aplacóforos registraron este patrón. En la región sur, se ha reportado la presencia de un giro ciclónico cuasi-permanente (Díaz-Flores et al., 2017) el cual promueve afloramientos de nutrientes que aumentan la productividad primaria y promueven una posterior exportación de MO al mar profundo. Asimismo, esta área se encuentra bajo la influencia del aporte de MO continental del sistema fluvial Grijalva Usumacinta, el segundo más importante en aporte de agua y sedimentos al GoM después del río Mississippi. Por otro lado, en la zona de domos salinos de la Bahía de Campeche se ha documentado la presencia de numerosas filtraciones de petróleo (Sahling et al., 2016). Los flujos naturales de petróleo pueden permitir el establecimiento de comunidades basadas en bacterias endosimbióticas quimioautotróficas, que no dependen de la exportación de materia orgánica producida en aguas superficiales o de la región continental (Levin y Michener, 2002; Levin, 2005; Bourque et al., 2017). Según MacDonald et al., (1989) en sitios cercanos a este tipo de ambientes suelen registrarse valores importantes de abundancia de infauna. En conjunto, estas condiciones ambientales podrían ayudar a entender el patrón geográfico de la abundancia. En la región noroeste del área de estudio, los valores intermedios y altos de abundancia podrían estar relacionados principalmente con la contribución de MO de la descarga de los ríos en las costas de Veracruz y Tamaulipas (por ejemplo, los ríos Soto la Marina, Pánuco, Tuxpan y Cazones).

Análisis multivariado

Los resultados del análisis multivariado mostraron diferencias en la composición y estructura de las comunidades de grandes grupos taxonómicos de la macrofauna, de familias de poliquetos y de familias de peracáridos, relacionados con cambios en la profundidad. Los cambios en composición y estructura de las comunidades de macrofauna a través de un gradiente batimétrico han sido documentados ampliamente en otras regiones de aguas profundas (por ejemplo, Levin et al., 2001; Bernardino et al., 2016; Woolley et al., 2016) y en el Golfo de México (por ejemplo, Hernández-Ávila et al., 2021). Es de resaltar que, a pesar de que los especímenes fueron identificados a un nivel taxonómico alto (grandes grupos o a nivel de familia), se logró detectar este patrón. Según Brandt et al., (2019) la identificación a nivel de grandes grupos taxonómicos puede no ser útil para mostrar las diferencias entre cuencas, pero suele ser suficiente para mostrar las diferencias entre distintas zonas de profundidad.

En el caso de los grandes grupos de la macrofauna, los taxones Polychaeta, Nematoda, Amphipoda, Isopoda y Bivalvia contribuyeron prácticamente en el mismo nivel a la abundancia general en las tres categorías de profundidad. Por lo que, las principales diferencias en la estructura de la comunidad relacionadas con la profundidad fueron influenciadas por la mayor contribución de Sipuncula y Ostracoda a la abundancia general de la UBZ en comparación con LBZ y AZ, mientras que Harpacticoida mostró una alta contribución a la abundancia general en las estaciones de las regiones batial inferior y abisal. Por otro lado, Tanaidacea, Porifera y Nemertea registraron un patrón de abundancia parabólico. En LBZ los dos primeros taxones presentaron la mayor contribución, mientras que el último fue mínima. En el caso de las familias de poliquetos, los principales cambios en la estructura de las comunidades estuvieron relacionados con la mejor representación de los espiónidos en UBZ; glicéridos y anfinómidos en profundidades intermedias (LBZ) y pilárgidos y longosomátidos en AZ. Los cumáceos solo se registraron en UBZ y LBZ y mostraron una ligera disminución de su abundancia relativa a medida que aumentó la profundidad. Los tanaidáceos presentaron mayor abundancia relativa en LBZ mientras que los anfípodos la registraron en UBZ y AZ. Los cambios en la comunidad de familias de peracáridos a través del perfil batimétrico se deben en mayor medida a la mejor representación de Apseudidae en LBZ, mientras que Phoxocephalidae, Tanaellidae y Agathotanaidae registraron mayor abundancia en UBZ y LBZ que en AZ. Caprellidae, Nototanaidae y Nannoniscidae registraron sus mayores abundancias en LBZ y AZ. Los isópodos de la familia Desmosomatidae fueron más abundantes en UBZ y AZ, los extremos del intervalo de profundidad estudiado. Según Frutos y Jażdżewska, (2019), las condiciones donde se asientan los caprélidos son apropiadas para los filtradores, mientras que en las zonas donde hay una menor proporción de sedimentos finos es más favorable para taxones de infauna como Phoxocephalidae. Esto podría explicar en parte la distribución observada de estos taxones. En UBZ la tasa de sedimentación es mayor que en AZ (Díaz-Asencio et al., 2019) lo cual podría implicar un ambiente menos favorable para los organismos filtradores en UBZ, mientras que en AZ podría ser más favorable. En el análisis sedimentológico se registró un aumento en el contenido de arcilla y una disminución en el contenido de limo al aumentar la profundidad, lo cual podría favorecer el establecimiento de taxones como Phoxocephalidae en UBZ.

Los cambios batimétricos de las comunidades infaunales se han atribuido a varios factores. Entre ellos, las variaciones del tamaño de grano de sedimento, la disponibilidad de oxígeno (Etter y Grassle, 1992; Levin et al., 2001), el flujo de carbono orgánico (Hernández-Ávila et al., 2021) y la proximidad a las regiones de talud (Woolley et al., 2016). En nuestro análisis, los factores ambientales relacionados con la distribución de la fauna presentaron algunas diferencias en función del grupo en estudio.

En el caso de los grandes grupos de la macrofauna fueron: la temperatura, el oxígeno disuelto, los hidrocarburos policíclicos aromáticos, la materia orgánica y la profundidad. Todos ellos han sido registrados como factores que afectan la composición y estructura de comunidades bentónicas en aguas profundas (Cosson et al., 1997; Allen, 2008; Levin y Sibuet, 2012; Brown y Thatje, 2014; Bernardino et al., 2016; Brandt et al., 2018). En el caso de las familias de poliquetos, los factores ambientales mejor correlacionados con la distribución faunística fueron materia orgánica, oxígeno disuelto y latitud. La latitud también se ha relacionado con cambios en la composición de las comunidades de macrofauna bentónica (Gage, 2004; Poore & Wilson, 1993; Rex et al., 2005). Por sí sola registró el mayor valor de correlación (0.356). Con respecto a las familias de peracáridos y de aplacóforos, la profundidad y la temperatura mostraron alta correlación con la distribución de la fauna, además de la latitud en el caso de los primeros y de la granulometría del sedimento en el caso de los segundos. Temperatura, latitud y profundidad han sido registrados como factores estructurantes de comunidades de peracáridos de aguas profundas (p. ej., Brandt et al., 2007; Di Franco et al., 2021).

Estimadores de diversidad

El patrón batimétrico de la diversidad alfa fue similar en los análisis de grandes grupos de la macrofauna y de familias de poliquetos. Este patrón se corresponde con el frecuentemente observado en mar profundo y consiste en valores altos de diversidad en profundidades intermedias (2000-3000 m) y más bajos en las regiones batial superior y abisal (Rex, 1981; Ramirez-Llodra et al., 2010; Bernardino et al., 2016; Wei y Rowe, 2019). Algunos autores mencionan que la alta diversidad en la LBZ puede deberse a la superposición de las faunas de las zonas de mayor y menor profundidad (Levin et al., 2001; Snelgrove y Smith, 2002). La misma tendencia se ha registrado en el mar profundo de la región norte del GoM (Wei y Rowe, 2019). Esto sugiere que los procesos que controlan la diversidad en el bentos podrían ser similares en todo el Golfo. En nuestro estudio, este patrón fue consistente en los tres números de Hill estimados. En el caso de los peracáridos el patrón fue distinto. La diversidad mostró un patrón batimétrico, también consistente en los tres números de Hill calculados, decreciendo al aumentar la profundidad, lo cual concuerda con lo reportado por Golovan et al. (2013) en el talud continental y la región abisal del mar de Japón. Sin embargo, no siempre se registra una disminución significativa de la diversidad de peracáridos con el aumento de la profundidad (Brandt, 1997) ya que se ha registrado mayor diversidad y número de especies a mayor profundidad (Rehm et al., 2007) o mayor riqueza de especies a profundidades intermedias entre 1.200 y 1.500 m (Wilson, 2008) y alrededor de los 3.000 m (Brandt et al., 2007).Esto indica que el patrón batimétrico de la diversidad alfa depende, en parte, del taxón en estudio. Los cambios atribuibles a la región o al taxón objetivo se han documentado previamente (Brandt et al., 2007, 2009; Shantharam y Baco, 2020).

La distribución espacial de la diversidad para los grandes grupos de la macrofauna mostró los valores más altos en las regiones sur y oeste del área de estudio y algunos sitios de la región abisal. También el análisis con las familias de poliquetos mostró valores importantes de diversidad en algunos sitios de la planicie abisal la cual, suele caracterizarse por presentar bajas abundancias, pero una alta diversidad de la macrofauna. En este ambiente, la dominancia no es frecuente y es muy común registrar un solo espécimen de cada especie (Sanders, 1968; Rex, 1981; Ramírez-Llodra et al., 2010). En el caso de los poliquetos la región de domos salinos de la Bahía de Campeche y el Cañón de Campeche también registraron valores altos de diversidad. La acumulación de materia orgánica suele mencionarse como uno de los factores promotores de alta diversidad y puede ser una de las razones para explicar los valores de diversidad registrados en estas localidades. En el caso de los peracáridos, la diversidad no mostró un patrón geográfico claro. Sin embargo, se observó que los valores de diversidad relativamente bajos que se registraron en sitios cercanos a la línea de costa y en los cañones de Campeche y Coatzacoalcos podrían estar relacionados con la alta tasa de sedimentación registrada en estos sitios reportada por Díaz-Asencio et al., (2019) ya que se ha documentado baja diversidad y alta dominancia en comunidades de peracáridos ubicadas en áreas donde los procesos de erosión son más frecuentes (Almeida et al., 2017).

Este trabajo aporta información importante de la composición y patrones de distribución de los principales componentes de la macrofauna bentónica en una región de aguas profundas poco estudiada. Abona al entendimiento global del gran ecosistema que es el Golfo de México y constituye una línea base para posteriores estudios ecológicos en esta región.

Conclusiones

Este estudio contribuye sustancialmente al conocimiento de las comunidades de macrofauna en un área escasamente estudiada del sur del Golfo de México abarcando una amplia área geográfica e incluyendo todo el intervalo batimétrico del mar profundo de las aguas mexicanas del Golfo. Aporta información importante de la composición y patrones de distribución de los principales grupos taxonómicos de la macrofauna y constituye una línea base para posteriores estudios ecológicos en esta región. El análisis ambiental permitió caracterizar las regiones batimétricas definidas. La UBZ se caracterizó por importantes concentraciones de OD, salinidad, variaciones de temperatura y altos valores de MO, limo e hidrocarburos, así como bajas concentraciones de sedimentos de carbonato y arcilla. Por otro lado, LBZ y AZ presentaron altos valores de OD, salinidad y temperatura, bajos valores de MO, hidrocarburos y limo, altos valores de carbonato y arcilla en el sedimento. Los siguientes fueron los taxones registrados, entre paréntesis los grupos dominantes. Se reconocieron 25 grandes grupos taxonómicos de la macrofauna (poliquetos, nemátodos, anfípodos, tanaidáceos y bivalvos), 45 familias de poliquetos (Spionidae, Paraonidae, Capitellidae, Cirratulidae y Amphinomidae), 53 familias de peracáridos (Apseudidae, Phoxocephalidae, Caprellidae, Desmosomatidae y Nototanaidae) y 3 familias de aplacóforos (Prochaetodermatidae). La abundancia disminuyó al aumentar la profundidad. De manera general, los valores de abundancia más altos se ubicaron en sitios menos profundos en la región sur y cerca de la línea de costa. Por otro lado, los valores más bajos se reconocieron en los sitios de la región norte, particularmente en la zona abisal. Además, se registraron valores de abundancia intermedios en la zona de domos salinos de la Bahía de Campeche y en los cañones de Coatzacoalcos y Campeche. Observamos cambios en la estructura de la comunidad relacionados con la profundidad en todos los análisis, con excepción de las comunidades de familias de aplacóforos. Los principales estructuradores de los grandes grupos taxonómicos de la macrofauna fueron: oxígeno disuelto, materia orgánica, latitud, profundidad y temperatura. En el análisis a nivel de familia, los tres primeros fueron los mejor correlacionados con la distribución de las familias de poliquetos; los tres últimos con las familias de peracáridos y los dos últimos además de la granulometría del sedimento para las familias de aplacóforos. A nivel de grandes grupos taxonómicos, la mayor diversidad se reconoció en el sur y noroeste del área de estudio a profundidades medias. El patrón fue similar para las familias de poliquetos, pero además incluyó la zona de los domos salinos de la bahía de Campeche como una región con alta diversidad, así como algunos sitios de la región abisal. En el caso de los peracáridos, el patrón fue distinto. La mayor diversidad se registró en UBZ seguida de LBZ y la menor diversidad en AZ. Geográficamente los sitios de mayor diversidad se ubicaron en las regiones sur y oeste y en el área de domos salinos de la Bahía de Campeche. Para los aplacóforos, los valores más altos de riqueza taxonómica se registraron en sitios cercanos a la línea de costa a baja profundidad en la región sur del área de estudio. En el análisis de temporalidad, se observaron diferencias en la abundancia de la comunidad entre los cruceros SOGOM 3 y SOGOM 4 que pueden estar relacionadas con un efecto estacional.

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