Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California

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Meiofaunal biodiversity of deep-sediments from the Gulf of Mexico: a metabarcoding and morphological approach for the establishment of a baseline

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José Alejandro Cisterna Céliz

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Tesis defendida por

José Alejandro Cisterna Céliz

y aprobada por el siguiente Comité

Dr. Axayácatl Rocha Olivares
Director de tesis

Dra. Elva Guadalupe Escobar Briones

Dra. María Asunción Lago Lestón

Dr. Juan Carlos Herguera García

Dr. William Kelley Thomas

Dr. Gerardo Rivas Lechuga

Dr. Jorge Adrián Rosales Casián
Coordinador del Posgrado en Ecología Marina

Dra. Rufina Hernández Martínez
Directora de Estudios de Posgrado

Abstract of the thesis presented by **José Alejandro Cisterna Céliz** as a partial requirement to obtain the degree of Doctor of Science in Marine Ecology.

Meiofaunal biodiversity of deep-sediments from the Gulf of Mexico: a metabarcoding and morphological approach for the establishment of a baseline

Abstract approved by:

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Dr. Axayácatl Rocha Olivares

Thesis Director

Meiofauna is an ecological group composed by organisms whose size ranges from 20μm as a lower limit to 100μm as the upper limit. It is composed of a high diversity of taxa of which Nematoda is dominant in both abundance and biomass. Meiofauna plays important roles in the ecosystem such as the exchange of nutrients by bioturbation of sediment, remineralization of organic matter, therefore playing an important role in biogeochemical cycles. It also occupies an intermediate trophic level between the microfauna and macrofauna. Despite its great ecological importance, meiofauna has been little studied, a situation that becomes more evident if we focus on the meiofauna of deep-sea sediments. In this research we aimed to evaluate the biodiversity of the meiofauna of the sediments from the Gulf of Mexico, under two approaches, "classical" morphological approach and through the metabarcoding of the 18S ribosomal gene, to answer the following questions (i) Is there an association between the environmental variability of the Gulf of Mexico and the meiofaunal communities? and (ii) What is the influence of dispersal on community structures? For this, a total of 128 samples were collected from three regions of the Gulf: deep-sea, continental shelf of Yucatan and platform and northwest slope. First, the structure of the meiofaunal community and the nematofauna of gulf deep-sea sediments was evaluated under the morphological approach, in relation to a set of environmental variables. The results indicate that there is spatial and temporal heterogeneity in environmental conditions and that some of them, such as depth, inorganic carbon, carbon/nitrogen ratio, oxygen, and percentage of sand, have an influence on the abundance of the meiofaunal community. Nematodes were numerically dominant in all the sampling sites, and the majority of taxa shared bacterivory as feeding strategy. This trophic group also had the highest maturity index. The structure of the nematofauna was significantly related to environmental characteristics, but not the dispersal of the genera. Based on these results, we postulate that the meiofauna of the deep-sea sediments from Gulf of Mexico may represent a metacommunity following the species sorting model. Next, the structure of the meiofauna was evaluated in the three regions of the Gulf of Mexico under the molecular approach of metabarcoding. The results indicate that each geographical area shelters a different meiofaunal community and that these differences occur at the level of sequence variants (taxonomic list) and the proportions between them. On the other hand, phylogenetic analyzes suggest that the northwest region of the Gulf of Mexico is an intermediate evolutionary region between the platform of Yucatan and the deep sea and that, in addition, the lineages of these last two regions still have not diverged from the lineages found in the Northwest Gulf region. The general results of this research allow us to conclude that the structure of the meiofauna differs significantly at a regional scale (among the three regions analyzed here), but also at a habitat scale in deep-sea sediments. On the other hand, results are consistent with the existence of limited dispersal.

Keywords: Meiofauna, Nematofauna, Gulf of Mexico, Deep-sea, Metabarcoding.

Resumen de la tesis que presenta **José Alejandro Cisterna Céliz** como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina.

Biodiversidad de la meiofauna de los sedimentos profundos del Golfo de México: un acercamiento de metabarcoding y morfológico para el establecimiento de una línea de base.

Resumen aprobado por:

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Dr. Axayácatl Rocha Olivares
Director de Tesis

La meiofauna es un grupo ecológico compuesto por organismos cuyo intervalo de tamaño va desde las 20μm como límite inferior hasta 1000μm como límite superior. Está compuesto por una diversidad alta de taxa de los cuales Nematoda es dominante tanto en abundancia como en biomasa. La meiofauna desempeña funciones importantes en el ecosistema como por ejemplo el intercambio de nutrientes por la bioturbación del sedimento y la remineralización de la materia orgánica, por lo que cumple un papel importante en los ciclos biogeoquímicos. Además, ocupa un nivel trófico intermedio entre la microbiota y la macrofauna. A pesar de su gran importancia ecológica la meiofauna ha sido poco estudiada, situación que se hace más evidente si nos enfocamos en la de sedimentos del mar profundo. En esta investigación nos propusimos evaluar la biodiversidad de la meiofauna de los sedimentos profundos del Golfo de México, bajo dos aproximaciones, morfológica "clásica" y a través del metabarcoding del gen ribosomal 18S, para responder a las siguientes preguntas (i) ¿Existe una asociación entre la variabilidad ambiental del Golfo de México y las comunidades meiofaunales? y (ii) ¿Cuál es la influencia de la dispersión en las estructuras comunitarias? Para esto se colectaron un total 128 muestras de tres regiones dentro de la Zona Económica Exclusiva del Golfo de México: mar profundo, plataforma continental de Yucatán y plataforma y talud noroeste. En primer lugar se evaluó la estructura de la comunidad meiofaunal y de la nematofauna en los sedimentos profundos del Golfo bajo la aproximación morfológica, con relación a un grupo de variables ambientales. Los resultados indican que existe tanto heterogeneidad espacial como temporal en las condiciones ambientales y que algunas variables como la profundidad, el carbono inorgánico, la relación carbono/nitrógeno, el oxígeno y el porcentaje de arena tienen una influencia en la abundancia de la comunidad meiofaunal. Nematoda fue el taxón dominante en todos los sitios de muestreo, y presentó una estructura trófica dominada por bacterivoría, grupo trófico que también presentó el mayor índice de madurez. La estructura de la nematofauna se relacionó significativamente con las características ambientales, pero no así la dispersión de los géneros. Con base en estos resultados, nosotros postulamos que la meiofauna de los sedimentos profundos del Golfo de México se comporta como una metacomunidad y que sigue el modelo de selección de especies. En segundo lugar se evaluó la estructura de la meiofauna en tres regiones dentro de la Zona Económica Exclusiva del Golfo de Mexico, con la aproximación molecular a través de metabarcoding. Los resultados indican que cada área geográfica alberga comunidades meiofaunales diferentes y que estas diferencias se dan a nivel de las secuencias variantes (elenco taxonómico) y de las proporciones entre ellas. Por otro lado, los análisis de diversidad filogenética sugieren que la región noroeste del Golfo de México es una región intermedia evolutivamente entre la plataforma de Yucatán y el mar profundo y que, además, los linajes de estas dos últimas regiones aún no divergen de los linajes de la región noroeste del Golfo. Los resultados generales de esta investigación permiten concluir que la estructura de la meiofauna difiere significativamente a escala regional (entre las 3 regiones del Golfo analizadas), pero también a una escala de hábitat en el mar profundo. Además, los resultados son consistentes con la existencia de una dispersión limitada.

Palabras clave: Meiofauna, Nematofauna, Golfo de México, Mar profundo, Metabarcoding.

Dedication

A Mateo y Emma

Y a los que vendrán…

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Chapter 1. Introduction

1.1 Generalities of meiofauna

Meiofauna is an ecological group defined as an "assemblage of benthic metazoans that can be distinguished from macrobenthos by their small size" (Mare 1942). The range of sizes has undergone changes throughout the years of study and depending on the environment in which it is being analyzed. In coastal sediments, where the size of the organisms is greater, meiofauna includes all metazoans retained by a sieve with mesh size between 44 and 63 µm (Giere 2009); whereas in deep sediments (>200m) a lower limit from 20 to 44 µm has been proposed (Danovaro and Gambi 2002; Zeppilli et al. 2016). This ecological group is considered the most abundant and diverse in deep sea sediments (Giere 2009), and typically the meiofauna of the deep-sea sediments is composed mainly of Nematodes as the most abundant group, reaching proportions many times greater than 90%, followed by harpactidoid copepods and annelids (Lambshead 2004; Grove et al. 2006; Giere 2009), and by less abundant groups such as Arthropoda, Mollusca, Kinorhyncha, Gastrotricha, Tardígrada, Platyhelminthes, among others. The life cycle of meiofauna is characterized by lacking a planktonic larval stage, which represents a limitation in its dispersal capacity.

Meiofauna plays very important roles in sediments; it serves as food for higher trophic levels such as macrofauna, enhances the exchange of nutrients through bioturbation, and has an influence on remineralization processes in the sediment, by stimulating microbial activity through grazing and enhancing the assimilation of detritus by deposit feeders (Service et al. 1992; Meadows and Meadows 1994; Montagna et al. 1995; Moens et al. 2007; Pape et al. 2013). Indirectly, it also has an influence on the biogeochemical cycles through its contribution to the remineralization of carbon and nitrogen (Ingham et al. 1985; Heip et al. 1992); in addition, many studies have shown that meiofauna is useful as a bioindicator of pollution, disturbances and climate change (Balsamo et al. 2012; Pusceddu et al. 2014; Zeppilli et al. 2015).

1.2 Ecology of the meiofauna

Different studies have tried to describe the relationship between the community attributes of meiofauna and environmental factors, so far with contrasting results. For shallow meiofaunal

communities salinity, temperature and grain size of the sediment have an important effect, in particular grain size (Giere 2009). On the other hand, in deep-sea sediment communities sediment heterogeneity, productivity, food, dissolved oxygen and deep currents have a significant effect on meiofauna (Rowe et al. 2008; Wei et al. 2010).

There are few studies conducted on the ecology of the meiofauna compared to macro or megafauna (Rex et al. 2006). The investigations carried out in the deep ocean have been done, to a large extent, on the continental margins (Figure 1), and have evaluated abundance, biomass and community structure in light of different environmental factors such as bathymetric gradients, surface productivity, different types of sediment and different spatial scales, among others. So far, it is difficult to find generalities for this ecological group, except for the bathymetric gradient and at different spatial scales.

Soltwedel (2000), published a review that covers research on meiofauna from the continental margins from 1970s to the end of the 1990s. Their main focus was on the patterns of abundance and biomass along the bathymetric and horizontal gradients and the vertical distribution of the meiofauna in the sediment, as well as the seasonal patterns in different oceans (Atlantic, Northwestern Indian, North and southwest Pacific) in the Mediterranean Sea, and in different regions (polar, temperate, subtropical and tropical). The results of the investigations included in this review indicate that the abundance and biomass of the meiofauna decrease with increasing depth of the seafloor, which responds to the decrease of the organic matter influx with the depth due to the degradation processes of sinking particles in the water column. For the same reason, the abundance and biomass of the meiofauna show differences not only with the depth of the water column, but also among areas with different regimes of primary productivity.

Rosli and coworkers (2018), published a review including the work done after the review of Soltwedel (2000), with a focus on patterns of spatial distribution of the deep-sea meiofauna at different scales: small (~0.1 – 10cm), local (~0.1 – 100m), habitat (~0.1 – 100km) and regional (~100 – 10,000km). Although community attributes such as abundance, diversity and community structure present a variation at all spatial scales, the greatest variability is generally observed at regional scale. As in the review carried out by Soltwedel (2000), differences at regional scale are mostly related to differences in surface productivity and physical disturbances; however, geological history and ocean currents can also contribute to regional patterns of distribution and abundance.

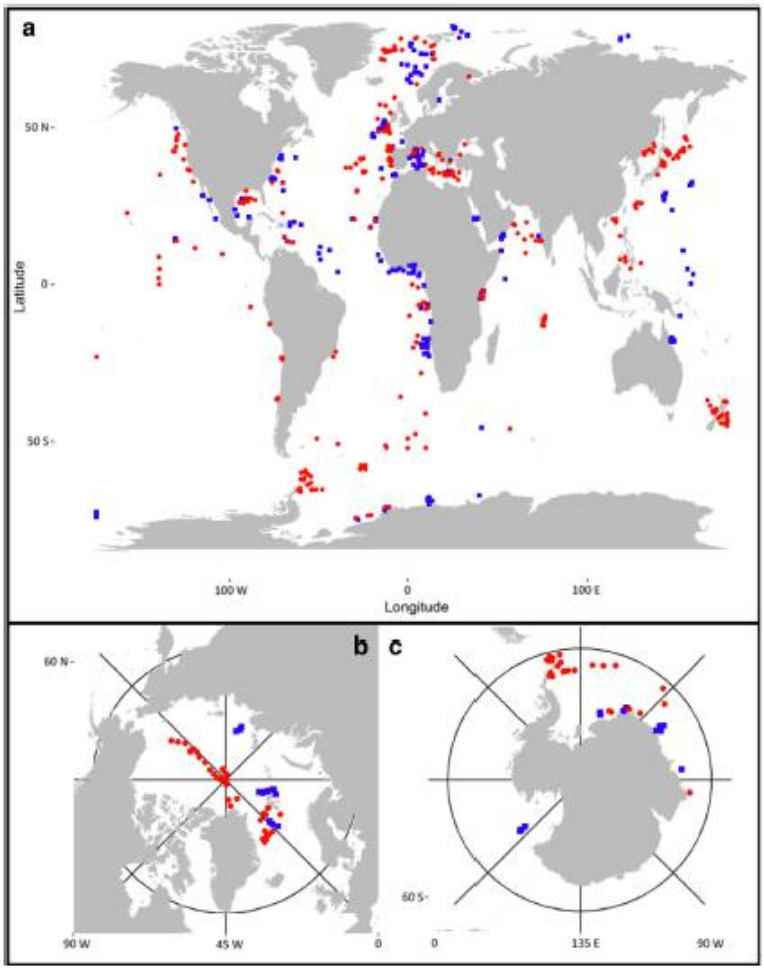

Figure 1. Map showing the distribution of the studies carried out in the meiofauna, before (blue circles) and after (red circles) of the review published by Soltwedel (2000). a) World Ocean, b) Arctic region and c) Antarctic region. Taken from Rosli and coworkers (2018).

Although dispersal would be expected to have very little influence in meiofaunal communities, given their lacking of a pelagic larval stage, the results until now are contrasting. Some agree that meiofaunal dispersal is important on a small scale; however, at larger scales it is the physical-chemical characteristics of the sediment that determine community structures (Fenchel and Finlay 2004; Leduc et al. 2012). On the other hand, others posit that deep-ocean meiofauna may have a high dispersal (Gallucci et al. 2008; Guidi-Guilvard et al. 2009; Guilini et al. 2011). For shallow sediments, analysis of genetic diversity suggests that population structures between patches separated by less than 1km are affected mainly by priority effects, founder effect and bottleneck processes (Derycke et al. 2013). On the other hand, because the absence of larval stage, passive dispersal by ocean currents has also been described as an important ecological process for meiofauna, particularly in shallow sediments (Palmer 1988; Radziejewska et al. 2006).

Historically, meiofauna has been studied through morphological observation through microscopes. This "classical" approach has generated much of the knowledge we have about this group until now, including not only the taxonomy, but also the trophic characteristics of groups such as nematodes (Wieser 1953). Recently, the study of these microscopic communities has been carried out using an approach known as "metabarcoding", which evaluates biodiversity using the DNA obtained directly from the environment (sediment in this case), and has become increasingly important in recent years because it allows access to the biodiversity of a sample in a simple way.

Research conducted on meiofauna using metabarcoding has revealed interesting results in terms of biogeographic patterns and bathymetric gradients suggesting that sediment depth has a greater influence on the community structure compared to sediments separated even by ocean basins suggesting a shorter coalescence time between deep-sea regions or slower rates of evolution across this ecosystem (Bik et al. 2010; Bik et al. 2012; Fonseca et al. 2014). In addition, this approach has revealed that the biodiversity found in molecular analyses is much higher than previously expected (Fonseca et al. 2017).

1.3 Meiofauna in the Gulf of Mexico

In the Gulf of Mexico (GoM) most of the research on meiofauna has been conducted in the US section. In this region of the Gulf, "The Deep Gulf of Mexico Benthos Program" stands out, which investigated the structure and function of the biota of the marine floor in the continental slope and abyssal plain (Rowe and Kennicutt 2008). This research program revealed that the biomass and respiration of meiofauna decrease with depth and that the highest levels were found in the vicinity of the Mississippi River in the continental slope; in addition, meiofauna respiration explained between 8 and 22% of all community respiration of sediments, reflecting the importance of meiofauna in diagenesis, carbon budget and global biogeochemical cycles (Baguley et al. 2008).

Additional research in the US section of the GoM revealed that the abundance of meiofauna is significantly related to the depth of the ocean and to a longitudinal gradient as well, the latter associated with the discharge of the Mississippi River, where the highest abundance was found in the canyon near the mouth of the river (Baguley et al. 2006; Sharma et al. 2011; Sharma et al. 2012). Regarding the nematofauna, the abundance on continental shelf correlates positively with high levels of aluminum and

silicate near the mouth of the Mississippi River, as well as with high levels of silt and clay; however, the abundance bears no relationship with depth (Beaton et al. 2018).

In the Mexican section of the GoM, differences in density and biomass of meiofauna have been documented between the western continental shelf and the southern Gulf. The highest values (5 to 6 orders of magnitude difference) were found in the shelf, where the sediment is dominated by clay and to a smaller proportion of sands. In both regions the dominant group were Nematoda and Copepoda (Escobar et al. 1997). Other research comparing the southwest continental shelf and the abyssal plain near the Sigsbee mound revealed slightly higher abundances in the southwest region, although differences were not significant. In terms of biomass, the abyssal plain presented higher values (Escobar-Briones et al. 2008). Regarding the nematofauna, De Jesús -Navarrete (1993) found 4 orders, 39 families, 86 genera and 96 species in the Campeche escarpment, which were distributed according to the sediment type, finding greater abundance in silty sediments than in sandy sediments. Soto and coworkers (2017) conducted another study in Mexico's exclusive economic zone of the Gulf (Perdido region). They evaluated the effect of the oil spill of April 2010 caused by the Deep Water Horizon oil platform on the nematofauna of the platform and continental slope of the northwest region of the Gulf. The results indicate that the nematofauna found in the summer of 2010 included 48 genera and an abundance of 44.45 ind $10cm^{-2}$, whereas 8 months later there was a decrease in the number of genera (23) and abundance (25.22 ind $10cm^{-2}$); however, in 2012 the nematofauna showed signs of recovery with a total of 58 genera and an abundance of 91.45 ind $10cm^{-2}$.

1.4 Generalities of the Gulf of Mexico

The sedimentology of the GoM is well characterized, from sediment transport and dispersion to mineralogy, the shape of grains, acoustic and geological characteristics of the sediment and chemical distributions (Trask 1953; Mazzullo 1986; Bouma et al. 1990; Twitchell et al. 1992).

Carbonate-rich sediments are present on the Florida and the Yucatan continental shelfs, whereas terrigenous sediments dominate the Texas-Louisiana-Mississippi shelf. The basal sediments reflect a mixture of these two major provinces, in addition to an input of pelagic sediments. The carbonate sands of the Yucatan shelf are mainly composed of ooids, fragments of skeletons (mollusks, foraminifera, echinoderms, corals, and bryozoans), pellets and carbonated clasts (Balsam and Beeson 2003). The

presence of carbonated mud is also found on this shelf, but it is subdominant to the sand.

Most of the Sigsbee abyssal plain is covered by marl, which is a mixture of pelagic carbonate sediments, principally foraminifera and coccolithophore and terrigenous clay, mainly from the Mississippi River. In the western section of the Sigsbee abyssal plain the relative contribution of pelagic organisms decreases and the terrigenous and calcareous clay takes on greater importance (Balsam and Beeson 2003) (Figure 2).

On the other hand, the Gulf of Mexico also has different physiographic regions (Figure 3). The continental shelf is almost continuous with a width that varies between 320km to 40km; the platform and continental slope present salt domes at different depths and important deposits of oil and natural gas associated with these. The abyssal plain is delimited by abrupt escarpments towards Florida and Yucatan and by gentler slopes in the north and west. The Sigsbee region is the deepest zone, where mounds are also found, which are the superficial expressions of buried salt domes (Martin and Bouma 1978).

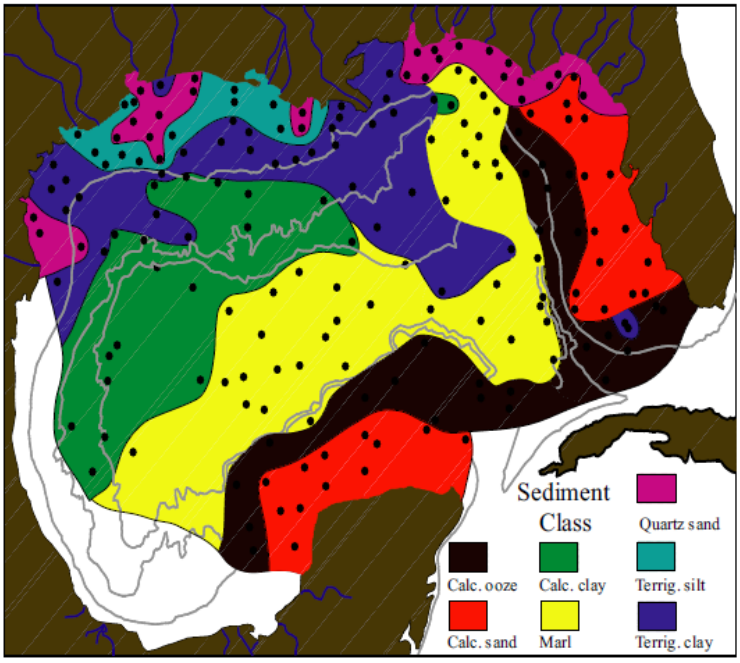

Figure 2. Distribution of the primary sediment classes of the Gulf of Mexico. Taken from Balsam and Beeson (2003).

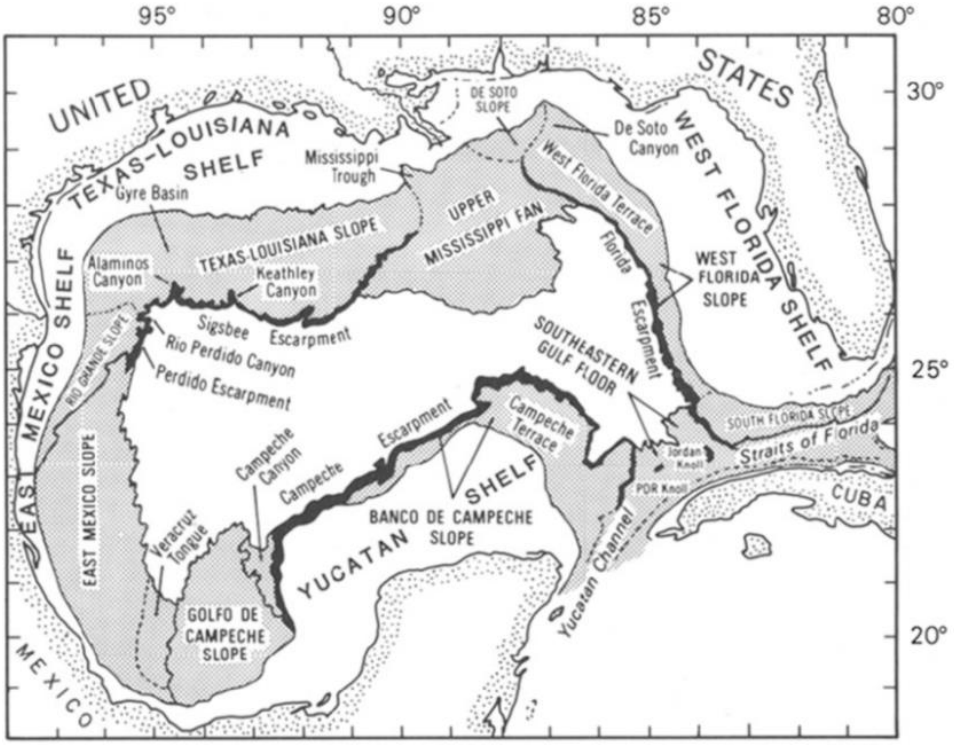

Figure 3. Physiographic regions of the Gulf of Mexico. Taken from Martin and Bouma (1978).

1.5 Justification

Meiofauna plays a very important role in marine ecosystems, from biogeochemical cycles to its position in the trophic web and utility as a bioindicator (Schratzberger and Ingels 2017). In order to better understand the role played by the meiofauna in these processes, it is necessary to first understand their patterns of abundance and distribution, which are influenced by external factors (environmental, sediment, bathymetry, among others) as well as internal (life history, trophic characteristics).

In this context, the Gulf of Mexico represents a unique environment for the study of these patterns since it presents contrasting regions with particular environmental characteristics, physiography, type of sediment and bathymetry.

1.6 Hypotheses

1.- Meiofaunal community structure will be affected by the environmental variability of the Gulf of Mexico

2.- Dispersal is not the main ecological process influencing community structure.

1.7 Objectives

1.7.1 General

Assess meiofaunal community of sediments from Gulf of Mexico under both morphological and molecular approaches.

1.7.2 Specifics

1.- Relate the meiofaunal abundance with environmental variability in deep-sea sediments from Gulf of Mexico.

2.- Evaluate the taxonomic and functional diversity of nematode community in deep-sediments from Gulf of Mexico.

3.- Evaluate meiofaunal community structure at large scale within the Gulf of Mexico (Yucatan shelf, northwest shelf and slope and deep-sea).

Chapter 2. Metacommunity analysis of meiobenthos of deep-sea sediments from the Gulf of Mexico

2.1 Introduction

A crucial question in ecology is how environmental drivers influence biodiversity patterns within and among communities. Diverse factors have been found to affect the communities inhabiting the interstitial space of marine sediments (i.e. including meiofauna). Salinity, temperature and sediment grain size have an effect on intertidal meiofauna, where sediment grain size is probably the most important (Giere 2009) . On the other hand, deep-water communities are more affected by sediment heterogeneity, productivity, food supply, bottom-water oxygen, deep-sea currents, and catastrophic disturbances (Rowe et al. 2008; Wei et al. 2010). Of these variables, it has been shown that depth has an important effect on abundance, diversity, and meiofaunal standing stock, given its influence on relevant environmental variables (Rowe et al. 2008; Giere 2009), whereas the other variables have been associated with patterns of horizontal zonation, biodiversity and ecosystem functioning (Gheskiere et al. 2004; Zeppilli et al. 2016).

Because of its ubiquity, meiofauna is considered a cosmopolitan ecological group; however, because of the limited dispersal capabilities of meiofaunal species, their apparent ubiquity gives rise to the “meiofaunal paradox” (Giere 2009; Boeckner et al. 2009).

Meiobenthic taxa are characterized by their short generation time; hence, they have a patchy spatial distribution with densities very difficult to predict, especially for deep-sea communities having been significantly less studied than coastal ones. In this regard, the existence of cryptic taxa has been revealed by genetic analyses in some coastal and recently described in Antarctic continental shelf nematode species; for example, remarkable changes in allele composition among adjacent populations have been shown in the cosmopolitan nematodes *Geomonhystera disjuncta* and *Pellioditis marina*, revealing metapopulation dynamics (Derycke et al. 2007; Derycke et al. 2008; Giere 2009; Hauquier et al. 2017).

Metapopulation theory is based on colonization and extinction dynamics of different patches containing local populations, where each of them could experience different dynamics implying some degree of demographic independence. This scenario assumes low levels of dispersal among local populations (Grimm et al. 2003). There are, at least, two main problems with the metapopulation approach in marine populations. First, the difficulty to delineate local and regional population boundaries as well as their spatial scale (Camus and Lima 2002), particularly for meiobenthic communities. Second,

for deep-sea meiobenthic communities, the difficulty of taxonomic identification to species level. On the other hand, meiobenthos may present different community structures, especially if the seabed morphology is irregular and sediment type is heterogeneous (Zeppilli et al. 2016), therefore it is possible to consider that different environments separated to regional scales (100's to 1000's meters) can shelter different meiofaunal communities.

Nematodes are the most abundant meiobenthic group (Baguley et al. 2006; Danovaro et al. 2008; Giere 2009). They are present in all environments and recent genetic evidence has shown that priority effects, founder effects and genetic bottlenecks may produce genetic structure in patches separated by less than 1 km (Derycke et al. 2013).

Nematodes possess a variety of life-history strategies and trophic habits. A maturity index (MI) was originally proposed to make inferences about ecosystem conditions based on the composition of nematode communities (Bongers 1990). It is based on categorizing nematode taxa along a colonizer-persister scale, reflecting thus if the dominant life history corresponds to a K- or r-strategy. Using this approach, the maturity state of different communities of marine nematodes has been assessed by the preponderance of persister organisms (Ingels et al. 2011; Bianchelli et al. 2013; Ürkmez et al. 2014; Fraschetti et al. 2016). On the other hand, the index of trophic diversity (ITD) (Wieser 1953), has been used to investigate the functional diversity of nematode communities. Hence, ITD allows testing diversity and ecosystem functioning hypotheses such as the positive correlation between biodiversity and ecosystem function and stability (Naeem et al. 2012; Mori et al. 2013), allowing to evaluate hypotheses of the relationship between environmental characteristics and proportions of each of the functional groups. Due to the fact that deep-sea nematode communities have been poorly characterized leading to a lack of identification keys, most ecological research of those communities is performed identifying specimens at the genus level. Hence, MI has been proposed for nematode genera, and even at family level for some groups (Bongers 1990; Bongers et al. 1991; Bongers and Bongers 1998).

Interactions among species result in ecological processes occurring at different spatial scales (Leibold et al. 2004; Storch and Gaston 2004), such as colonization and extinction patterns, demography of local communities influenced by movement of organisms from other communities, among others. Hence, the concept of metacommunity has been proposed to study the interaction of different species at a regional scale. A metacommunity (Leibold et al. 2004) has been defined as "a set of local communities that are linked by dispersal of multiple potentially interacting species", and it is based upon 4 simplified views, (i) the patch dynamics paradigm (PD), which assumes that each habitat patch is determined by

both stochastic and deterministic extinctions, interspecific interactions, and dispersal. Under this paradigm, regional coexistence is governed by interspecific competition for resources; (ii) the species-sorting paradigm (SS), which considers the effects of environmental gradients (local abiotic features) on population vital rates and species interactions; (iii) the mass-effect paradigm (ME), which refers to the source-sink relationships among populations in different patches as the result of dispersal, each patch having different conditions at a particular time such that it is possible to relate local conditions and community structure; and (iv) the neutral-model paradigm (NM), which is a null hypothesis for the other three paradigms (Leibold et al. 2004).

The study of community dynamics and its correlation with environmental factors remains a challenge, especially at different spatial scales. Metacommunity theory represents a very useful approach to explain patterns found in nature. Under a condition governed by patch dynamics (PD), dispersal is the main process in structuring communities given the absence of environmental heterogeneity among patches, the result being that species lacking high competitive ability may coexist on a regional scale. On the other hand, in the presence of environmental heterogeneity among patches, the SS paradigm proposes a discrete distribution of species whereas the ME paradigm predicts a more complex scenario, in which coexistence could be the result of a trade-off between local dynamics (such as predation) and dispersal (colonization-extinction dynamics). Finally, the NM paradigm results when environmental and biological dynamics bear no predictable power to explain metacommunity structure.

Since the difference between SS and ME paradigms is the relative importance of dispersal, and taking into consideration that dispersal rates remain unknown in deep-sea meiobenthos, we posit that the extent of change in community structure could be a proxy for the degree of isolation between them. One of the most used concepts to analyze differences in community structure is β diversity (Ellingsen 2002; Koleff et al. 2003; Fontana et al. 2008; Dimitriadis and Koutsoubas 2011; Gambi et al. 2014), defined by Whittaker (1960) as the change of community composition or differentiation in relation to environmental gradient. Many expressions have been proposed to quantify β diversity emphasizing different aspects (Koleff et al. 2003); nonetheless, β diversity measures species substitution and species loss (or gain) among communities (Carvalho et al. 2012).

Here, we study the meiofaunal community structure from the deep GoM under the framework of metacommunity dynamics. The GoM has been subdivided into physiographic regions according to prevailing environmental factors, such as sediment type. For instance, the northern section of the abyssal plain has sediment of continental origin in which the carbonate content is less than 25% (Bouma 1972;

Escobar-Briones et al. 2008), whilst the sediment of the central and south sections of the abyssal plain has a hemipelagic origin, and is mainly composed of pelagic foraminiferan shells (Escobar-Briones et al. 2008). The central and southern parts of the Sigsbee Abyssal Plain, which is the deepest and flattest sector of the northwestern Gulf of Mexico, are relatively enriched in carbonate (30-50%) with respect to lower continental slope environments surrounding it, and they consist mostly of a mud relatively enriched with planktic and benthic foraminiferal shells and coccoliths [for a thorough environmental description of the GoM see: Escobar et al. (1997); Escobar-briones et al. (1999)].

We hypothesize that environmental variability will have an effect on total meiobenthic community, and that particular environmental characteristics will reflect on different nematode communities. For the first hypothesis, we relate environment features with total community abundance, and for the second hypothesis we analyze the functional structure of nematode community and its maturity stage (MI and ITD indices), as well as the β diversity to estimate dispersal. Given that the deep GoM has different sediment types, we expect that nematode community structure can be explained by the SS or ME paradigms.

2.2 Material and Methods

2.2.1 Field sampling

Deep-sea stations (1233 – 3738 m) were visited in the Mexican economic exclusive zone (EEZ) of the GoM, during the course of XIXIMI Cruises led by the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE) on board the R/V Justo Sierra (Universidad Nacional Autónoma de México). A total of twenty-seven sediment cores were collected during XIXIMI-1 (X-1 henceforth, n = 7, November 2010), XIXIMI-2 (X-2 henceforth, n = 11, June 2012) and XIXIMI-3 (X-3 henceforth, n = 9, February 2013) cruises. With the aim of sampling most of the GoM, sampling stations were located in different physiographic and sedimentary regions (Martin and Bouma 1978; Balsam and Beeson 2003). Due to sampling constraints only one core was sampled at each station, however, physiographic regions were sampled more than once in each cruise and some stations were revisited in different cruises (Fig. 4).

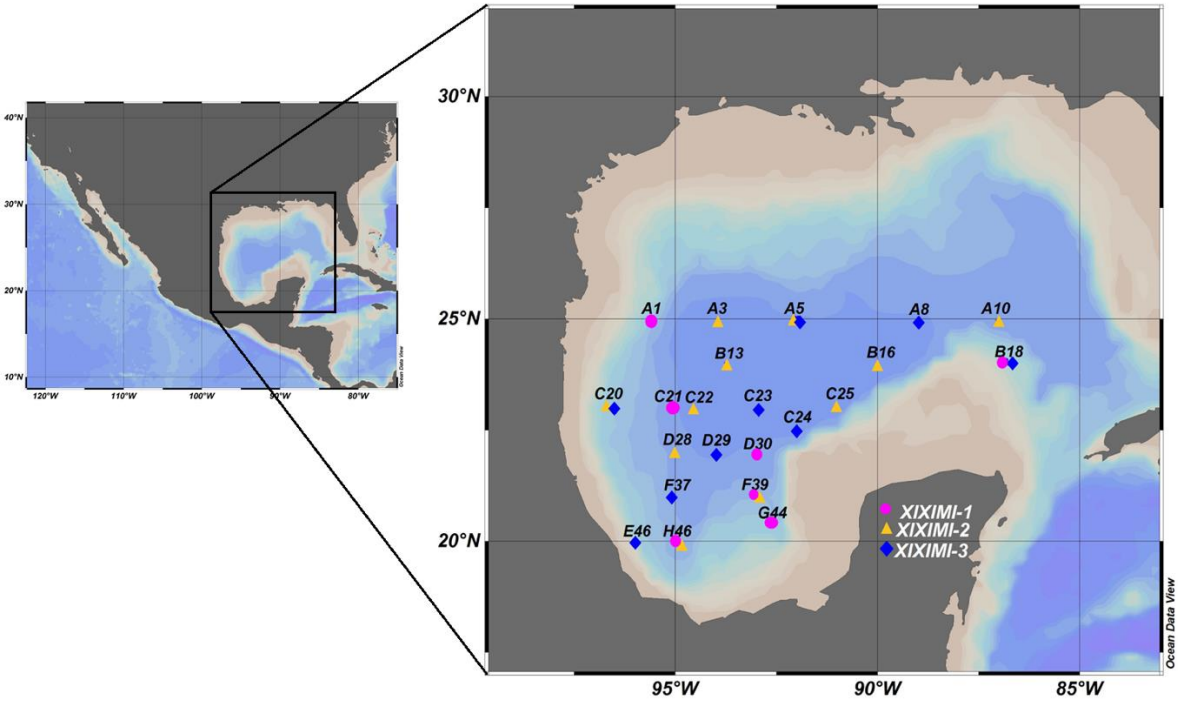

Figure 4. Sampling stations within Gulf of Mexico. Pink circles: stations for X-1, yellow triangles: stations for X-2 and blue diamonds: station for X-3. Some stations were sampled twice in different years. Figure created using Ocean Data View (versión 4.5.6, Schlitzer, R. 2013. http://odv.awi.de)

Samples (12cm-deep cores) were taken using either a box-corer, from which cylindrical sediment cores were subsampled with an acrylic core (internal diameter 8.1 cm, X-1), or using a multicorer device deployed to the deep-sea (internal diameter 10 cm, X-2 and X-3). Sediment was preserved in 10% buffered formalin.

2.2.2 Meiofauna extraction

Meiofauna was extracted from the sediment matrix by decantation and flotation with colloidal silica (Ludox ™, specific gravity 1.15g cm^{-3} (de Jonge and Bouwman 1977) followed by sieving through a 1000 µm mesh, and retained on a 45 µm mesh (Somerfield and Warwick 1996). The process was repeated three times to maximize the number of extracted organisms. Once separated from sediment, organisms were stored in 10% buffered formalin in a final volume of 40ml.

2.2.3 Organism quantification and identification

Fixed organisms were resuspended and ten of the 40 ml (aliquots of 25%) containing the meiofaunal community were mounted on permanent slides for quantification, identification and archival. Slide mounting involved previous glycerol impregnation (45% water, 50% alcohol, 5% glycerin). In addition, the remaining 75% of the sample (30 ml) was analyzed in cruises X-2 and X-3.

Meiofauna from all cruises was identified to major taxa using a Primo Star microscope (Carl Zeiss) following the descriptions in Giere (2009). In addition, a subset of nematodes from the X-1 cruise (10% per station) were randomly selected and taxonomically identified to genus level under an Olympus-BX51 microscope using the marine nematode taxonomic keys Platt and Warwick (1983), (1988); Warwick et al. (1998) and the Nemys database (*http://nemys.ugent.be/*). Identified nematodes were classified into four functional groups: 1A selective deposit feeders, 1B non-selective deposit feeders, 2A epistrate or epigrowth feeders and 2B predators/omnivores (Wieser 1953).

2.2.4 Ecological analyses

We computed diversity as genus richness (S), equitability (J) and Shannon-Wiener (H') indices for each sample from X-1. To estimate the life-strategy dominance of the nematode community, each genus was assigned a colonizer-persister (c-p) score, as detailed in Bongers (1990); Bongers et al. (1991); Bongers and Bongers (1998). Subsequently, the maturity index (MI) was computed as the weighted mean of c-p scores: MI = Σ υ (i) * f (i), where υ is the c-p value of genus i as given in the Appendix of Bongers et al. 1991), and f (i) is the frequency of that genus. In this way, communities with an MI close to 1 will be composed mainly of colonizers and communities with an MI close to 5 will be composed mainly by persisters. Nematode functional diversity was estimated using the Index of Trophic Diversity (ITD) as 1 – ITD, where ITD = $\theta_1^2 + \theta_2^2 + \theta_n^2$, θ is the relative contribution of each trophic group to total abundance, and n in the number of trophic groups (Gambi et al. 2003). For n = 4 (as in the present study), values range from 0 (lowest trophic diversity, only one trophic group) to 0.75 (highest trophic diversity, where each of the four trophic groups are equally abundant) (Bianchelli et al. 2013).

2.2.5 Environmental analyses

Granulometric analyses were conducted for each core using a laser particle size analyzer HORIBA LA910. Sediment from the three cruises was classified as (i) very fine silt, (ii) fine silt, (iii) coarse silt, and (iv) very coarse silt. For cruises X-1 and X-2 only the % of sand, silt and clay were determined. Total organic carbon was measured on acidified samples in an elemental analyzer (COSTECH™) coupled to a continuous flow mass spectrometer Delta V™ with an analytical error of ±0.05 %. Carbonate values were measured on a coulometer UIC Model 5014 with an analytical error of 0.1%.

Dissolved oxygen was measured by an oxygen sensor (SBE43) connected to a SEABIRD9 CTD which was calibrated with microWinkler measurements on board the ship. The measurements reported were taken usually 20 m above the bottom.

2.2.6 Data analyses

In order to analyze abundance patterns, we first estimated the total abundance from the aliquots analyzed in the X1 cruise. For this we regressed abundance from the entire sample as a function of abundance estimated from the 25% aliquots in cruises X2 and X3, and used the linear equation to estimate total abundance for X1 samples.

The first step to apply the metacommunity theory is to establish if the environmental variables are spatially heterogeneous and to determine if the environmental variability is related to meiobenthic community. Hence, a Principal Components Analysis (PCA) was conducted using log-transformed and normalized data. To relate meiobenthic abundance with environmental variables, Canonical Analysis of Principal Coordinates (CAP) was conducted on meiobenthic abundance using the components obtained from PCA. CAP analysis is a constrained ordination analysis that takes into account the correlation structure among the variables in the predictor data (Anderson and Willis 2003) and generates scores that were used in correlation analyses with the total abundance of meiobenthos. Finally, in order to assess spatial autocorrelation of environmental variables, we computed Moran's I Index (Moran 1950) using the package Moran.I in R (Team 2013).

Subsequently, we used PERMANOVA to assess the effect of sampling time and sediment classification on total abundance of the meio- and nemato- fauna. Time was considered as first factor (3 levels: 2010, 2012 and 2013) and sediment classification as second factor (4 levels: very fine silt, fine silt, coarse silt and very coarse silt). A posteriori pair-wise tests were performed to identify significant terms. All analyses were carried out using PRIMER 6 & PERMANOVA+ software packages (Anderson et al. 2008).

2.2.7 β diversity

To evaluate dispersal among communities, β diversity was used as a proxy. The premise being that diversity (i.e., community differentiation) would increase with increasing distance as the result of decreasing dispersal and increasing isolation. Many indices have been proposed to measure β diversity (Koleff et al. 2003). In this paper we analyze β_{cc} as defined by Colwell and Coddington (1994) (Equation (1)), partitioning it into two components: (i) replacement between two sites (β_{-3}) (Equation (2)), and (ii) species richness differences (β_{rich}) (Equation (3)), as proposed by Carvalho et al. (2012). All pairwise β diversity estimates (β_{-3} and β_{-rich}) were correlated to geographic distance between stations through Mantel test using Pearson's correlation with 10000 permutations in R package (Team 2013). The expressions are as in Koleff et al. (2003).

$$\beta_{cc} = \beta_{-3} + \beta_{rich} \quad (1)$$

and

$$\beta_{-3} = 2\,x\,\frac{min(b,c)}{a+b+c} \quad (2)$$

$$\beta_{rich} = \frac{b-c}{a+b+c} \quad (3)$$

where: *a* is the number of shared genera between sites 1 and 2, *b* is the number of exclusive genera from site 1, and *c* is the number of exclusive genera from site 2.

Because the northwest section of the GoM and the Yucatan Peninsula are only represented by one sampling station each, we performed non-parametric bootstrap to geographically balance the number of samples and increase the number of observations from undersampled regions (namely where A1 and B18

are located) (Huang and Chi 2012). We resampled 1000 random iterations with replacement using the abundance of individual genera to estimate the 95% confidence limits (c.l.) of correlations between beta diversity and geographic distance using R software (Team 2013).

2.2.8 Environmental differences among sampling stations

In order to evaluate if the environmental differences have an effect on nematode communities and identify which metacommunity paradigm may explain our findings, we correlated environmental distance (Euclidean distance) among sampling stations with geographic distance (shorter waterbone distance between any two samples) as well as with β diversity through a Mantel test as in the previous β diversity analyses. First, environmental distance (including all environmental variables) between station pairs was correlated with geographic distance, to test for an environmental gradient. Second, to test if the environment differences among sampling stations have an effect on community structure, we correlated the environmental distance between sampling stations (calculated from the scores of CAP 1 of X-1 CAP analysis) with β_{cc} diversity. Environmental distance was calculated using PRIMER 6 & PERMANOVA+ software packages (Anderson et al. 2008).

2.3 Results

2.3.1 Meiobenthic community

As expected, the regression between abundance from entire samples and from 25% aliquots of X-2 and X-3 was linear, significant ($R^2 = 0.83$; $p < 0.01$, 95%, Fig. 5), and was used to estimate the abundances for the total of X-1 samples for subsequent analyses.

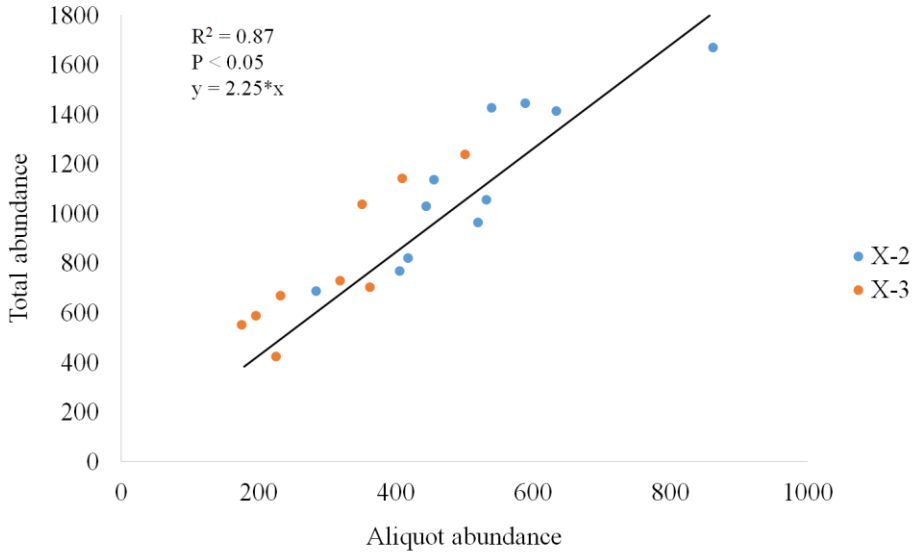

Figure 5. Regression analysis of meiofaunal abundance in the entire sample (total abundance) against estimated from 25% (aliquot abundance) in samples from X-2 and X-3 cruises to estimate total abundance in X-1 samples. Blue circles: X-2 and Orange circles: X-3.

We identified a total of 17 major taxa (X-1:7; X-2: 12; X-3: 17): Nematoda, Copepoda, Ostracoda, Oligochaeta, Polychaeta, Platyhelminthes, Gastrotricha, Tardigrada, Loricifera, Tanaidacea, Hydrozoa, Nemertea, Isopoda, Asteroidea, Kinorhyncha, Sipuncula and Acari (Appendix 1, App henceforth). Localized temporal variation was evident; for instance, station C22 possessed the highest abundance in X-1 but one of the lowest in X-2; inversely, in station H46 meiofauna abundance increased from X-1 to X-2. In stations A8 and A5, abundance decreased from X-2 to X-3, whereas in station B18 it increased from X-1 to X-3.

Community structure was dominated by nematodes in all samples exceeding 80% in most of them, followed by Copepoda, Platyhelminthes, and Oligochaeta in X-1, and Copepoda and Platyhelminthes in X-2 and X-3, except that in X-3 Platyhelminthes outnumbered Copepoda, whereas the other major taxa were rare in all cruises.

2.3.2 Environmental variation and community correlates

Different environmental characteristics at each sampling station and for each cruise were found, which is one of the prerequisites for SS and ME dynamics (App 2). The first two principal components (PC)

accounted for 73.5% of the variance of environmental variables from X-1; nevertheless, three PC's were significant based on eigenvalues greater than one. PC1 accounted for 53.2% and had negative loadings with longitude, %sand and inorganic carbon, and had positive with depth, %silt, %clay and total organic carbon. PC2 accounted for 20.3% and had negative loading with C/N ratio and positive loadings with latitude, sediment classification and oxygen (Fig. 6a). In the PCA analysis of X-2 environmental variables, the first two components accounted for 66.4% of total variance, although four PC's were significant. PC1 accounted for 43.8% and had negative loadings with %silt, longitude and depth, while PC2 accounted for 22.6% and had negative loading with %sand and positive loadings with total organic carbon and depth (Fig. 6b). Finally, in X-3 the first two components accounted for 71.3% of total variance of environmental variables. PC1 accounted for 43.2%, had negative loading with inorganic carbon, and positive loadings with total organic carbon and longitude. PC2 accounted for 28.1% and had negative loadings with oxygen, depth and latitude, and a positive loading with carbon/nitrogen ratio (Fig. 6c). PCA results suggest that sediment characteristics (%silt and %sand) and depth are the main environmental factors contributing to environmental heterogeneity among sampling stations.

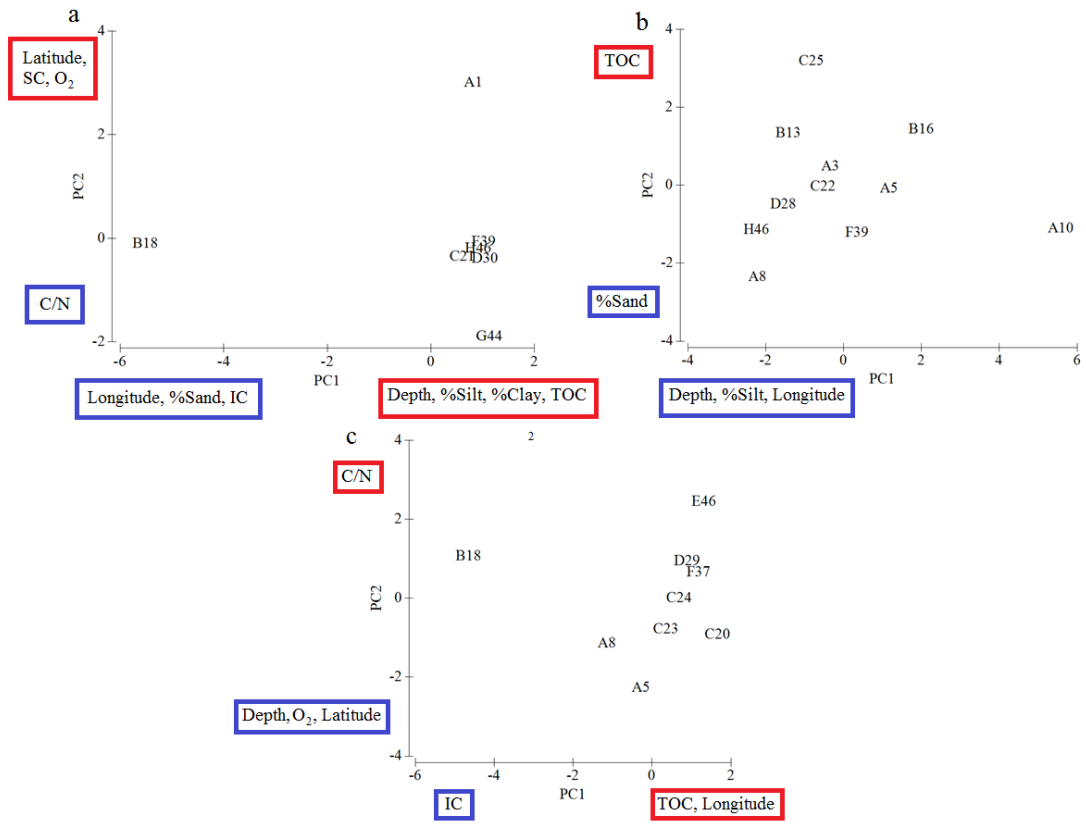

Figure 6. PCA analysis of environmental variables for each cruise. a) X-1, b) X-2 and c) X-3. C/N: Carbon/Nitrogen ratio, TOC: Total Organic Carbon, IC: Inorganic Carbon, SC: Sediment Classification. Red rectangles mean positive loadings and blue rectangles mean negative loadings.

Meiofaunal abundance correlated significantly with certain CAP scores, with the first in X-1 and with the second in X-3 (Fig. 7). In X-1, the relation was negative ($r = -0.76$; $p < 0.05$) and the CAP had negative loadings with inorganic carbon, oxygen and %sand, and positive loadings with depth and latitude (Fig. 7a). In X-3, the relation was positive ($r = 0.73$; $p < 0.05$) and the CAP had negative loadings with total organic carbon and depth, and positive loading with inorganic carbon (Fig. 4c). On the other hand, in X-2 the relation was positive and nearly significant ($r = 0.48$; $p = 0.066$) (Fig. 7b).

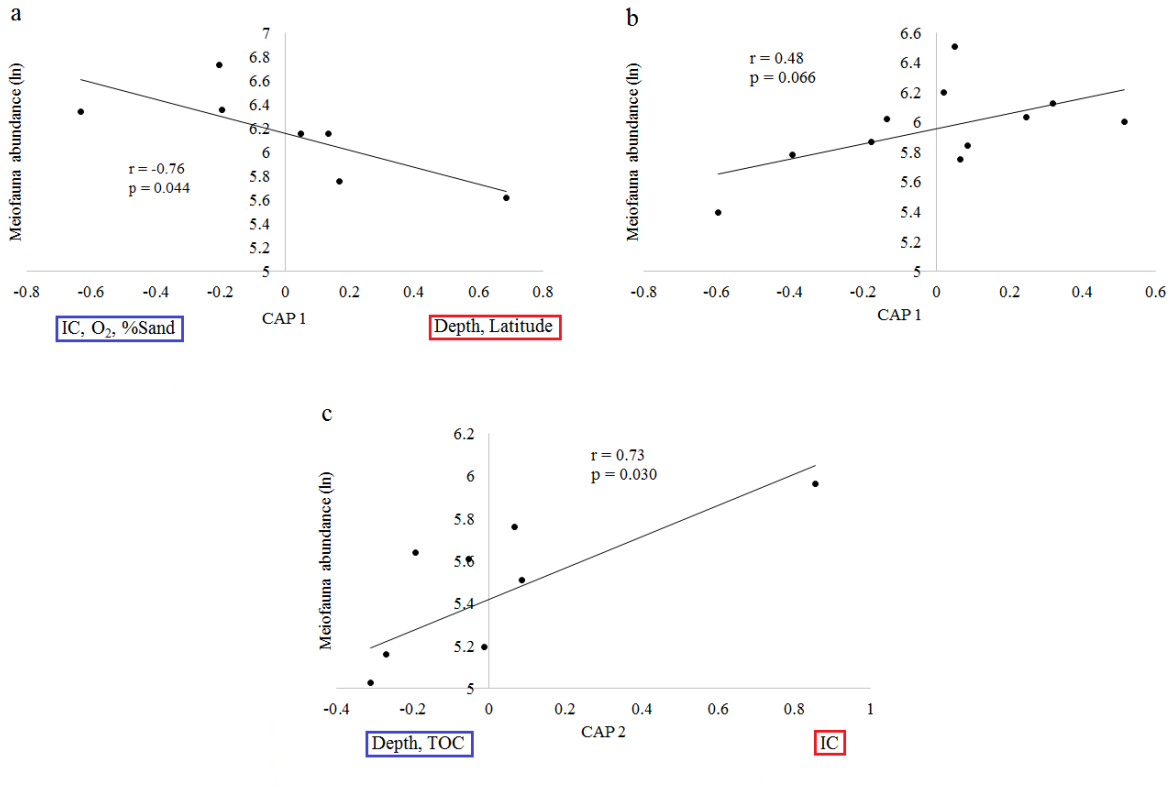

Figure 7. Meiofauna abundance (ln) correlated against environmental CAP. a) X-1, b) X-2 and c) X-3. TOC: Total Organic Carbon, IC: Inorganic Carbon. Red rectangles mean positive loadings and blue rectangles mean negative loadings. Loadings in X-2 are not included because the correlation was not significant.

Hence, depth was a factor that correlated significantly with meiobenthos abundance (X-1 and X-2), as expected, and a significant influence of environmental characteristics on total meiobenthic abundance was found as expected for SS or ME metacommunity models.

PERMANOVA analyses revealed significant effects of time x sediment interaction for total meiofaunal abundance (pseudo-$F = 3.53$, $p < 0.05$) (Table 1). Pair-wise tests showed that differences in

total abundance were found between X-1/X-3 cruises, and temporal differences involved stations dominated by fine silt (level 2 of the factor "sediment type") located in a sedimentary classified as Marl (Balsam and Beeson 2003), indicating that observed differences occur within and not among sedimentary regions.

Table 1 PERMANOVA summary results for Total Abundance by sample and Total Abundance of Nematoda by sample. Cr: cruise, Se: sediment (4 levels of silt).

	Source	Df	MS	Pseudo-F	p (perm)
Total Abundance by Sample	Cr	2	38.521	3.586	**0.039**
	Se	3	20.303	1.89	0.154
	CrxSe	3	37.973	3.535	**0.027**
	Res	18	10.741		
	Total	26			
Total Abundance of Nematoda by sample	Cr	2	246.4	16.814	**0.0002**
	Se	3	12.361	0.84351	0.502
	CrxSe	3	57.09	3.8957	**0.0246**
	Res	18	14.655		
	Total	26			

2.3.3 Nematofauna

Differences among nematode community structures were found in samples from X-1. A total of 70 genera belonging to 30 families were found of which Cyatholaimidae was the most diverse family, whereas Aphelenchoididae was represented by a single dominant genus (App 3). Forty-nine percent of identified organisms were distributed among 9 genera: *Aphelenchoides*, (12.9%), *Microlaimus* (7%), *Desmoscolex* (6%), *Halalaimus* (5.8%), *Molgolaimus* (3.9%), *Diplopeltula* and *Amphimonhystrella* (3.4% each one), *Aponema* (3.2%) and *Pselionema* (2.9%).

Only three of the most abundant genera were found in all sampling stations: *Microlaimus*, *Desmoscolex*, and *Halalaimus,* and these last two belong to functional group 1A and have an M.I. of 4, which means that they are bacterivorous and persistent genera. Diversity analyses of all nematode

communities indicate that B18 was the most (H' = 5, S = 37) whereas C21 was the least diverse station (H' = 3.8, S = 17) (Table 2).

Table 2. Nematode community attributes for XIXIMI-1. S: genera richness, J: equitability, H': Shannon-Wiener diversity (log2).

Sampling Station	Depth (m)	S	J	H’
A1	2416	37	0.94	4.88
B18	1233	39	0.94	4.98
C22	3569	17	0.93	3.81
D30	3297	19	0.95	4.04
F39	2549	22	0.85	3.77
G44	2464	21	0.89	3.91
H46	2758	32	0.93	4.64

2.3.4 Index of trophic diversity and maturity stage of communities

Taxonomic differences among nematode community were reflected in differences of trophic diversity and maturity stages. The nematode community with a higher ITD was found in A1, B18 and C22, meanwhile the communities with lowest ITD were found in F39 and H46 (Fig. 8a) and that pattern was not correlated with depth. Functional group 1A was the most abundant (>=50% in all sampling stations) indicating the prevalence of bacterivory as well as algal-derived phytodetritus feeders in those communities, followed by groups 2A, 1B and 2B (Fig. 8b). MI values were higher than 2.6 (G44) but lower than 3.10 (H46) in all communities indicating that their maturity is limited. In other words, they are composed by a mixture of persister and colonizer genera (Fig. 8c). Finally, the MI calculated for each functional group revealed that 1A and 2B are composed by more persistent organisms, as opposed to 1B and 2A groups, composed of a larger fraction of colonizers (Fig. 8d).

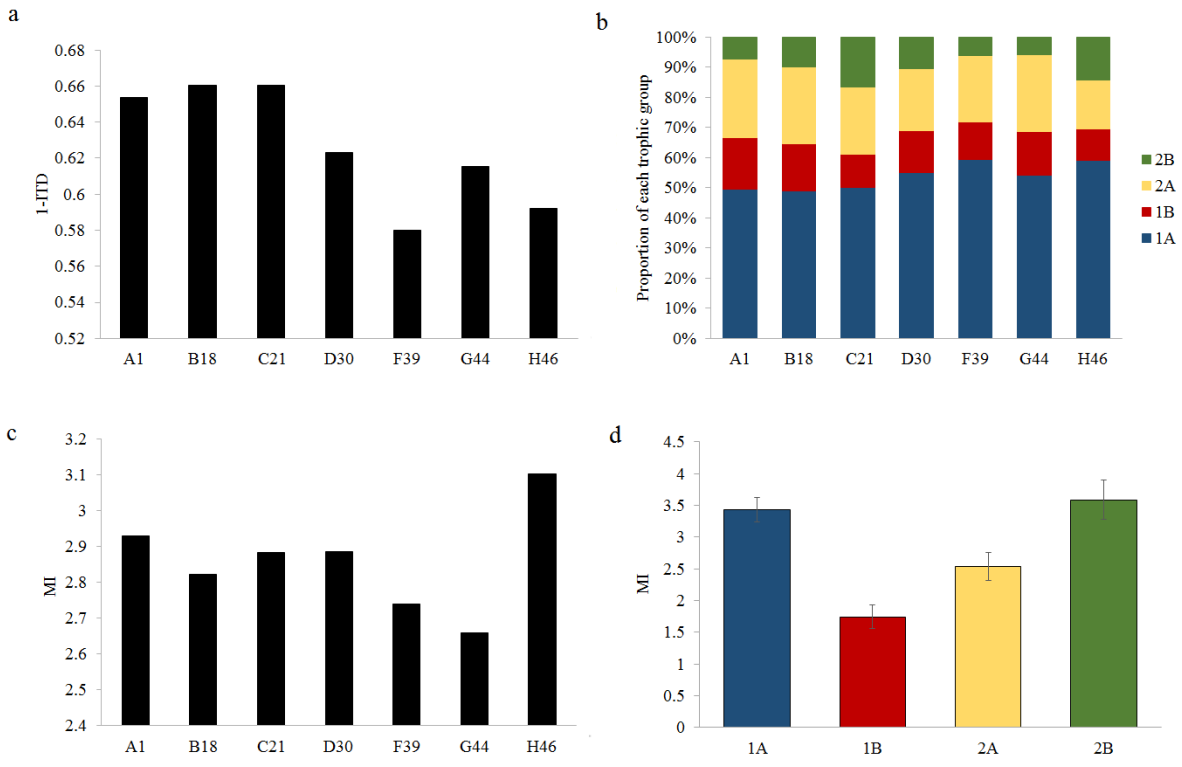

Figure 8. Index of trophic diversity (1-ITD) and maturity index (MI) for nematode communities from X-1. a) ITD at each sampling station, b) proportion of trophic groups at each station, c) MI at each sampling station and d) MI at each functional group. In figure b, 1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epistrate or epigrowth feeders and 2B: predators/omnovires.

PERMANOVA disclosed significant effects of time x sediment interaction on total abundance of nematodes (pseudo-F = 3.89, $p < 0.05$) (Table 1). Differences in total abundance were found between X-1/X-3 and X-2/X-3 cruises only for comparisons among stations dominated by fine silt (level 2 of the statistical factor).

2.3.5 β diversity and environmental differences among sampling stations

The β_{-3} index does not appear to bear a significant relationship with geographic distance overall; however, a closer inspection reveals two groups of data, one defined by sampling stations C21, D30, F39, G44 and H46 (group 1, henceforth) and another by stations A1 and B18 (group 2, henceforth). In each of those groups diversity did correlate directly with geographic distance (Fig. 9a) (group 1: $r = 0.74$, $p < 0.05$,

bootstrap c.l. 0.40 – 1; group 2: r = 0.65, p < 0.05, bootstrap c.l. 0.18 - 1), suggesting different processes of replacement. β_{rich} showed a positive relation with geographic distance overall (r = 0.65, p < 0.05, bootstrap c.l 0.33 – 0.94) indicating that differences in genus richness increase with geographic separation (Fig. 9b). The total compositional difference among nematode communities β_{cc} did not show a significant relationship with geographical distance (Fig. 9c), but structural differences increase rapidly between nearest sites up to 400 km, after which large differences in community structure are maintained. These patterns reflect a break in β_{-3}, suggesting the existence of different processes acting on the nematode communities at two spatial scales. Hence, results of β diversity indicate that dispersal is limited among sampling stations of the GoM and that community structure is influenced by other ecological process.

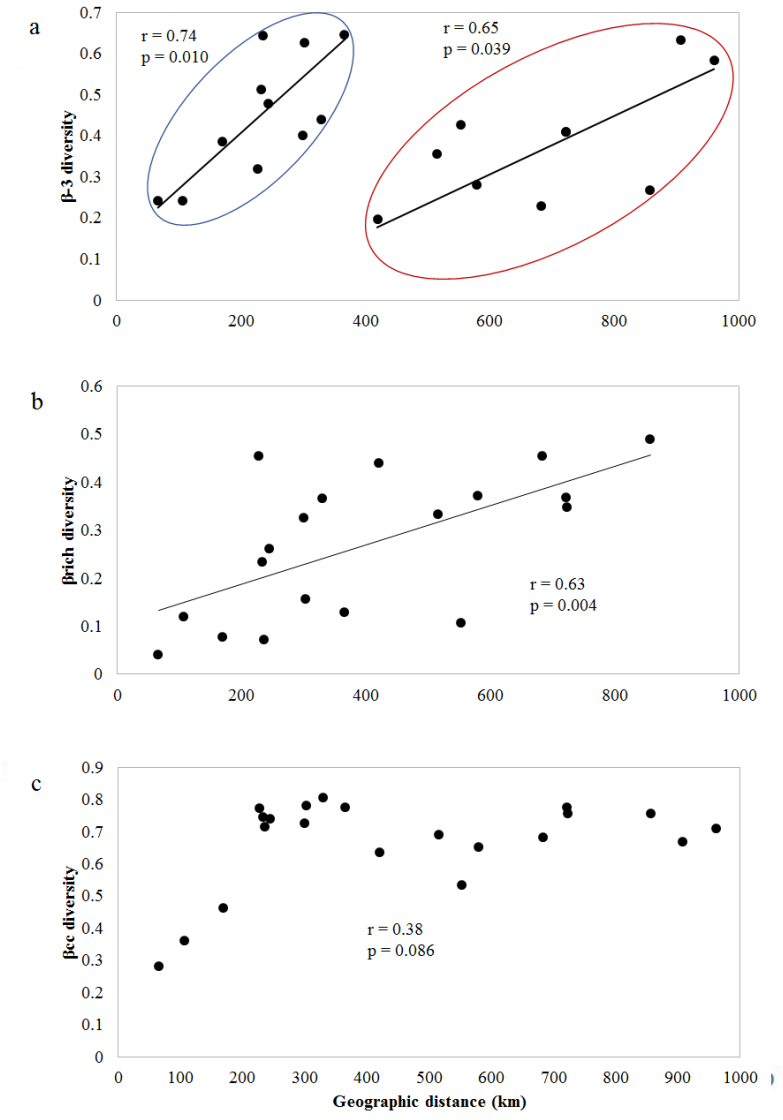

Figure 9. β diversity results correlated with geographic distance (Km). a) β_{-3} diversity, b) β_{rich} diversity and c) β_{cc} diversity. In figure a) blue circle include paired comparisons of sampling stations C21, D30, F39, G44 and H46 (group 1) and red circle include comparisons with sampling stations A1 and B18 (group 2).

Environmental distance among sampling stations, including all environmental variables, was positively correlated with geographic distance (Fig. 10a) ($r = 0.87$, $p < 0.01$) and all environmental variables did not display a significant spatial autocorrelation (Moran's I between -0.06 and -0.33). This finding indicates that environmental differences increase with an increasing geographic distance between stations. On the other hand, we found a positive correlation between environmental distance and β_{cc} (Fig. 10b) ($r = 0.65$), $p < 0.05$). The environmental distance reflects changes in the variables included in the CAP1 of the CAP analysis for X-1. Consequently, this result suggests that differences in community structure (β diversity) are influenced by environmental differences among sampling stations.

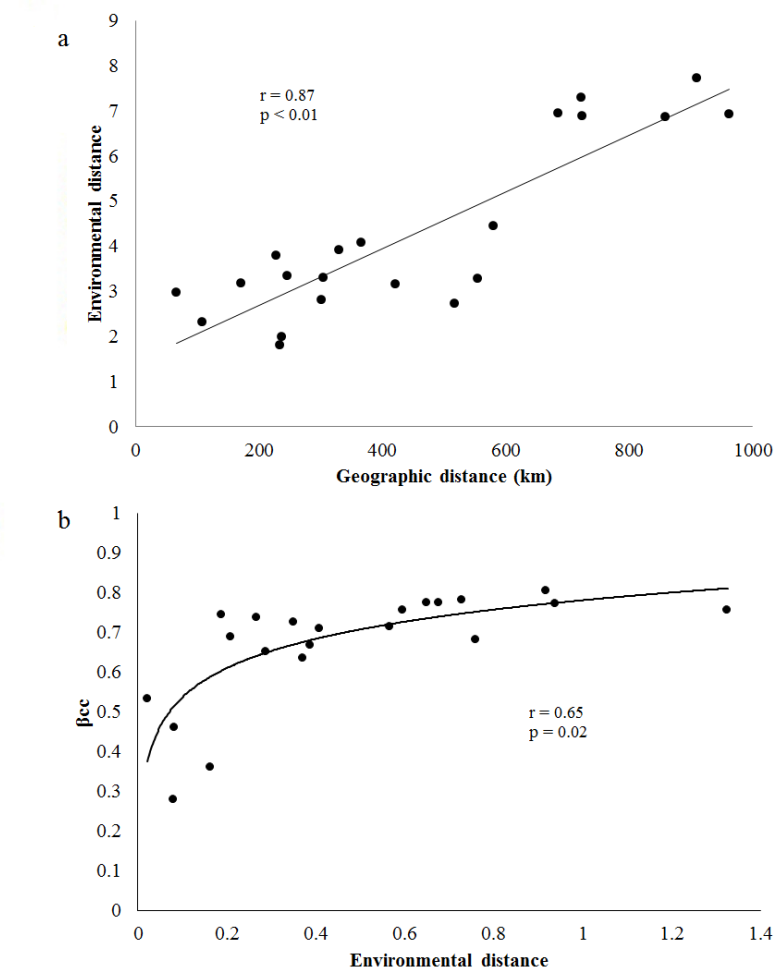

Figure 10. Euclidean distance (E. D.) of environmental variables from paired-comparisons of all sampling stations from X-1. a) E.D. including all environmental variables, and b) E.D. of scores from CAP analysis of X-1.

2.4 Discussion

2.4.1 Environmental features of the GoM

Metacommunity theory is based on the notion of spatial heterogeneity in environmental attributes, such as the one found in the GoM. Relevant for the infauna is the existence of sedimentary provinces characterized by different sediment types, such as calcareous and carbonate sands, carbonate mud, terrigenous and hemipelagic sediments (Bouma 1972; Escobar et al. 1997; Escobar-briones et al. 1999; Balsam and Beeson 2003; Escobar-Briones et al. 2008). Our results suggest that sediments sampled at each station represent environments differing in environmental attributes, such as: 1) composition (i.e., percent of sand and silt), 2) organic and inorganic carbon content, 3) oxygen availability of bottom waters and 4) depth (Fig. 6). These factors have been found to contribute to the environmental heterogeneity of other deep-sea sediments, and to have a strong influence on the structure of meiobenthic communities and turnover of nematode assemblages (Gambi et al. 2014; Gambi and Danovaro 2016; Zeppilli et al. 2016). Our results show differences in community structure within the sediment type known as Marl, suggesting that the combination of environmental drivers are modulating the community structure. A patch-mosaic model has been proposed for deep-sea soft-sediment communities to explain the high species richness despite the apparent physical homogeneity (Gallucci et al. 2008; Gallucci et al. 2009). In this model, patches are the result of differential input of organic matter and disturbance. Thus, our results suggest that each sediment core is a sample of a distinct environment, and could also be a sample of a local patch of meiobenthos.

2.4.2 Total community abundance

The association between environmental variables and the structure and function of a community has remained a challenge in ecology; because a variety of drivers can influence community dynamics in different ways. Nevertheless, community patterns found in this research are related to some environmental drivers in consistence with metacommunity theory. Most researchers consider trophic conditions as the main factor that determines meiobenthic abundance. A review analyzing the general patterns of meiobenthos distribution on a global scale found significant positive relationships between chloroplastic pigment equivalents content, organic matter flux and quantity and quality of sedimentary organic matter, related to nematode abundance (Mokievskii et al. 2007; Rosli et al. 2018). Likewise, sediment size and type may be important in structuring meiobenthic communities and in determining

seafloor heterogeneity (Zeppilli et al. 2016). In this regard, our results of meiobenthic community abundance showed a significant correlation with these sediment properties (Fig. 4). In general terms, our results show that meiobenthic abundance decreased with increased depth in all cruises, and also increased with increasing total organic carbon in X-3. On the other hand, meiobenthic abundance decreased with decreasing inorganic carbon, oxygen, carbon/nitrogen ratio and increased sediment size (%sand).

Depth is the main factor influencing the meiobenthic abundance, estimations of particulate organic carbon (POC) flux from surface water of the northern U.S. section of the GoM suggest an export of about ~18 mg C m^{-2} day^{-1} in the NE, 1.85 mg C m^{-2} day^{-1} in the NW and ~9 mg C m^{-2} day^{-1} for the continental slope in the NW section, while in the central Gulf an export of about ~3 mg C m^{-2} day^{-1} has been estimated (Biggs et al. 2008; Stuart et al. 2017). Hence, depth is correlated with a decrease in POC export from surface to the deep-sea and with decreased meiobenthic abundance (Baguley et al. 2006).

2.4.3 Total community structure

Nematoda, Copepoda and Platyhelminthes were the most abundant groups in all sampling periods; whereas Gastrotricha, Oligochaeta, Polychaeta, Loricifera, Tardigrada, among others, were rare, as has been described in other deep-sea sediments (Mokievskii et al. 2007; Rosli et al. 2018). Nematodes have been recognized as the most abundant group in meiobenthic communities, almost always exceeding 75% of the total number of meiobenthic organisms (Giere 2009; Rosli et al. 2018). However, values as low as 50% have been found at depths exceeding 1000m in oligotrophic areas of the central Arctic Basin, in the tropical central part of the Indian Ocean and in the tropical Atlantic (Soltwedel 1997; Ansari 2000; Ingole et al. 2000), with low meiobenthic abundance (<100 ind 10 cm^{-2}). In this study, nematode prevalence exceeded 80% and community structure was similar to other deep-sea sediments. In contrast, differences were found among sediment samples characterized by fine silt and belonging to the same sedimentary type within the Gulf (Balsam and Beeson 2003), suggesting that sediment type is not the main factor influencing the community structure, but has a synergic effect with other environmental drivers (Table 1).

2.4.4 Nematode community: Functional and maturity stage

Feeding strategies of nematofauna have been shown to vary with depth, mostly due to morphological differences, as well as their abundance and diversity influenced by organic matter input to the sediment (Sharma et al. 2012). We found that ITD and the proportion of functional groups of nematode communities are similar among samples. Sampling stations with the highest ITD were A1, B18 and C22, which means that the abundance of the four functional groups is more even compared with the other sampling stations, a pattern bearing no association with depth. The fact that most nematodes (>=50% in all sampling stations) belong to group 1A reflects the prevalence of bacterivory in deep-sea communities. It has been suggested that greater ocean depths harbor smaller bacterial cells in benthic environments of the GoM and that bacterial biomass declines significantly with depth (Deming and Carpenter 2008). In contrast, no significant relationship has been found between bacterial abundance and biomass with depth, according to a random forest model for the same region (Wei et al. 2010). The preponderance of trophic group 1A in nematode communities suggests that the trophic web supporting them is based on bacterial production as the most important resource; on the other hand, the MI values between 2.6 and 3.1 of the same communities indicate that they are composed by an admixture of colonizer and persister genera. Nevertheless, the MI of each trophic group revealed that groups 1A and 2B are comprised of more persister and mature genera (Fig. 8d). On the other hand, groups 1B and 2A are characterized by colonizer organisms (Bongers 1990).

On the other hand, the low abundance of the genera belonging to groups 1B, 2A and 2B may reflect the small amount of available resources for those trophic groups, and therefore, the low carrying capacity of the environment.

Although metacommunity theory proposes that community structures could be different depending on environmental features and on ecological processes such as dispersal, the function and maturity stage of the communities we analyzed are similar. This finding suggests that deep-sea meiobenthic functional structure and complexity may be independent of environment or ecological factors.

2.4.5 Nematode community: dispersal and environmental differences

Given the environmental differences among sampling stations, the SS or ME paradigms of metacommunity theory could be evoked to explain the patterns of nematode abundance and community structure (Leibold et al. 2004; Logue et al. 2011). The difference between these paradigms is the relative importance of dispersal; SS assumes that dispersal is sufficiently low to allow species to fill up niches within habitat patches via niche diversification, thereby species may coexist. On the other hand, ME assumes that dispersal among patches is large enough to cancel local dynamics. Deep-sea meiobenthic dispersal rates are unknown; hence, differentiating between SS and ME paradigms remains a considerable challenge. Our results of β diversity analyses suggest a low level of dispersal among nematode communities (Fig. 9c), as it has been already reported for nematodes (Fenchel and Finlay 2004; Leduc et al. 2012), and its partition in replacement and richness suggests that compositional differences among sites (β_{cc}) are the result of different processes governing community structure in different regions of the Gulf (Fig. 9).

Based on our results we may suggest a close relationship between environmental characteristics and nematode community structure (Fig. 10b), this is a significant but not strong asymptotic relation that may suggest that environmental variability and dispersal have a synergic influence on nematode communities. Our results show a geographic separation of sampling stations A1 and B18 with the rest, station B18 is characterized by the highest percent of sand and its sediment was classified as very coarse silt, whereas station A1 was classified as very fine silt. Station B18 is where we found the highest number of genera and exclusive ones (39 and 14 respectively). This is concordant with the observed pattern in shallow waters that sandy sediments shelter higher nematode diversity levels than silt or clay (Giere 2009). On the other hand, the remaining sampling stations have a sediment classified as fine silt, and are located in a sediment region described as marl (Balsam and Beeson 2003), which is an admixture of pelagic carbonate sediment, foraminifers and coccoliths, and terrigenous clay. Thereby, the similarity of communities separated by less than 200 km (Fig. 9c) may be due of sampling stations sharing a similar environmental features but after that, communities may be influenced by a limited, but still present, passive dispersal of organisms.

2.5 Conclusion

Here, we were able to use the metacommunity theory to analyze the meiobenthic and nematode communities of the GoM and to evaluate if communities are influenced by environmental, ecological or a combination of both factors. Our results suggest that based on the predictions of metacommunity theory, nematode communities from the deep GoM may conform to the SS model. This inference is based on the different taxonomic structures among sampling stations correlating with environmental differences, in the presence of local niche diversification and limited dispersal. Our results support the idea that deep-sea meiobenthic communities may be organized as metacommunities, nevertheless further studies at the species level are needed.

Chapter 3. Metabarcoding analysis of the meiofaunal communities from the Gulf of Mexico

3.1 Introduction

The main goal of ecology is the determination of the patterns and forcing of the distribution of species, populations and communities. While it is true that there is still no consensus on the explanation of the patterns found in nature, some theories that try to explain them range from niche theory (Tilman 1982) to neutral theory (Hubbell 2001). For macroscopic organisms (plants and animals) these patterns are understood relatively well; however, for microscopic organisms such as those included in the meiofauna, it still represents a challenge (Lambshead and Boucher 2003). The α and β diversity patterns of meiofauna can be affected by intrinsic characteristics, as well as by external factors. Meiofauna is composed of different phyla that have particular characteristics, among which are (i) short generation time, which is one of the reasons that the meiofauna has a patchy distribution; (ii) absence of a larval stage, which entails a low dispersal potential; (iii) another factor influencing the distribution of communities and their biodiversity is the suite of interactions among populations; it has been described that direct interactions between meiofaunal groups result in competition, niche partition and/or exclusion (Giere 2009). Regarding environmental factors, it has been reported that the frequency of disturbances in the sediment will define the dominant life strategy, in addition, the depth of the water column, type of sediment, and heterogeneity of the marine floor have a significant influence on the abundance and distribution of the meiofauna (Baguley et al. 2006; Giere 2009; Zeppilli et al. 2016).

In recent years, efforts to understand the distribution patterns of meiofauna in the deep ocean have increased, both with traditional and molecular methods (Mokievskii et al. 2007; Bik et al. 2012; Fonseca et al. 2017). These efforts, in turn, have revealed large gaps in the taxonomy of these organisms (Sinniger et al. 2016). Some studies have described that the deep-sea meiofauna have cosmopolitan distributions alluding to the environmental stability of this region of the ocean with respect to shallow sediments. Indeed, it has been reported that the seafloor depth represents a limitation for the distribution of the species, much greater than geographical distance (Pawlowski et al. 2007; Aldea et al. 2008). On the other hand, it has been described for the Mediterranean bathyal sediments that the α diversity patterns follow gradients of trophic conditions (Bianchelli et al. 2013); it has also been described that environmental heterogeneity has a positive influence on biodiversity and ecosystem functioning because this heterogeneity allows different communities along different habitats, thus increasing diversity on a

regional scale (Zeppilli et al. 2016). Therefore, the analysis of communities that inhabit sediments with different environmental characteristics and located at different seafloor depths provide an important opportunity to characterize the distribution patterns and, in turn, understand them under the light of environmental variability.

3.1.1 Metabarcoding: biodiversity from DNA

Historically, meiofauna has been studied from the morphological description of organisms; however, the current advent of massive DNA sequencing platforms has been the gateway to the intensive study of biodiversity in microscopic communities. The application of these sequencing techniques to characterize the diversity of an environmental sample has been called "metabarcoding" and has become increasingly important in the description of eukaryotic communities, including the meiofauna (Bik et al. 2012; Fonseca et al. 2014; Lallias et al. 2015). The analysis of these data involves the formation of operational taxonomic units (OTUs) grouping sequences that differ by less than a certain threshold, generally 3% at the species-level; nevertheless, it has recently been proposed that the use of OTUs should be replaced by exact variant sequences (SVs) since they distinguish sequences that differ up to one nucleotide (Callahan et al. 2017). Thus, the SVs have greater sensitivity and specificity than the OTUs and can discriminate community patterns at finer scales.

So far, the research carried out using this approach has generated important information on the distribution of meiofauna at the habitat (~ 0.1 – 100Km) and regional scales (~100 – 10,000Km), and one of the main results found among samples from the Pacific and Atlantic ocean basins is that the bathymetric gradient has a greater influence than interoceanic geographical separation per se on the distribution of some meiobenthic groups (Bik et al. 2010; Bik et al. 2012).

3.1.2 Sedimentary environments of the Gulf of Mexico

In the GoM, the presence of different physiographic regions is a source of variability of the sedimentary habitat inhabited by meiofauna, each region is defined by the type of predominating sediment: calcareous sands, carbonated sands, carbonated mud, terrigenous and hemipelagic sediments

(Bouma 1972; Martin and Bouma 1978; Escobar et al. 1997; Escobar-briones et al. 1999; Escobar-Briones et al. 2008).

In sedimentary terms, the gulf is basically divided into two primary provinces: terrigenous sediments from the continent to the north and west of the gulf, and carbonate sediments that originate in the Florida and Yucatan continental shelfs (Ward and Tunnell 2017). The sedimentary deposits of the western GoM receive isolated allochthonous contributions while in the Yucatan platform they are autochthonous (Escobar et al. 1997), the western region is the result of several factors: (i) tectonic dynamics, (ii) coastal current, (iii) displacement of sediments from rivers that flow into the gulf whose sediments contribute to the formation of a fringe of terrigenous sandy sediments with a carbon content smaller than 25% (Pica-Granados et al. 1991; Escobar et al. 1997). The continental contribution of the southern region on the continental shelf and slope is insignificant due to the absence of surface rivers and the relief caused by weathering (Bouma 1972; Escobar et al. 1997). On the other hand, the deep environment of the gulf is dominated by sludge in a combination of terrigenous and biogenic sediments that include coccolithophorids, foraminifera, diatoms and radiolaria (Ward and Tunnell 2017).

The investigations on the meiofauna of the GoM have been carried out mostly in the US section. For this region of the GoM, the presence of 21 taxonomic groups has been reported and studies indicate that there is a significant decrease in the abundance and biomass of meiofauna with increasing seafloor depth, as well as a longitudinal gradient resulting from the proximity to the mouth of the Mississippi River (Baguley et al. 2006; Baguley et al. 2008; Sharma et al. 2012; Beaton et al. 2018). In Mexican waters, the study of meiofauna has been scarce; 14 taxonomic groups have been reported and available studies indicate that depth has an effect on abundance, although not significant. Moreover, biomass tends to be higher in the abyssal plain compared to the southwestern region (Escobar et al. 1997; Escobar-Briones et al. 2008). Regarding the nematofauna, the presence of 86 genera and 96 species in the Campeche bank have been reported, which are distributed according to the sediment (de Jesús-Navarrete 1993). On the other hand, a research conducted by Soto and coworkers (2017) did explore the nematode genera in deep sediments after the oil spill of the Deep Water Horizon platform in 2010. Results indicates that the amount of genera in 2010, 2011 and 2012 were 48, 23 and 51 respectively.

Due to the scarcity of information on meiofauna in the Mexican section of the GoM and the sediments characteristics of its physiographic regions, in this research we address the following questions: What is the structure of the meiofaunal community in different geographical areas of the Gulf of Mexico? Is there dispersal between these areas? To answer these questions, the meiofaunal community was

evaluated in three geographic areas from the GoM: the Yucatan continental shelf, the northwest slope and shelf (Perdido), and the deep-sea, using metabarcoding. Our hypothesis is that each of the environments will shelter different communities and that dispersal between them is very low.

3.2 Material and Methods

3.2.1 Sampling

The gulf was sampled in 4 regions of the Mexican exclusive economic zone: deep sea, northwestern slope and shelf ("Perdido region" henceforth) and Yucatan platform, in the oceanographic campaigns XIXIMIs, Perdido and GOMEX, repectively (Figure 11). The first was led by the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE) while the second and third were by the Centro de Investigación y Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV), on board the R/V Justo Sierra (Universidad Nacional Autónoma de Mexico). A total of 128 sediment cores were collected during the 3 campaigns: 62 cores from the deep sea (966 - 3739 m depth, average 2858 m ± 927 m SD) during six XIXIMI campaigns between November 2010 and August 2017; 48 cores from the Perdido region (44 - 3466 m depth, average 1281 m ± 1034 m SD) during the two Perdido campaigns in May and November 2016, and 18 cores in the Yucatan platform (16 - 220 m depth, average 73 m ± 54 m SD) in August-September of 2016 (App. 4).

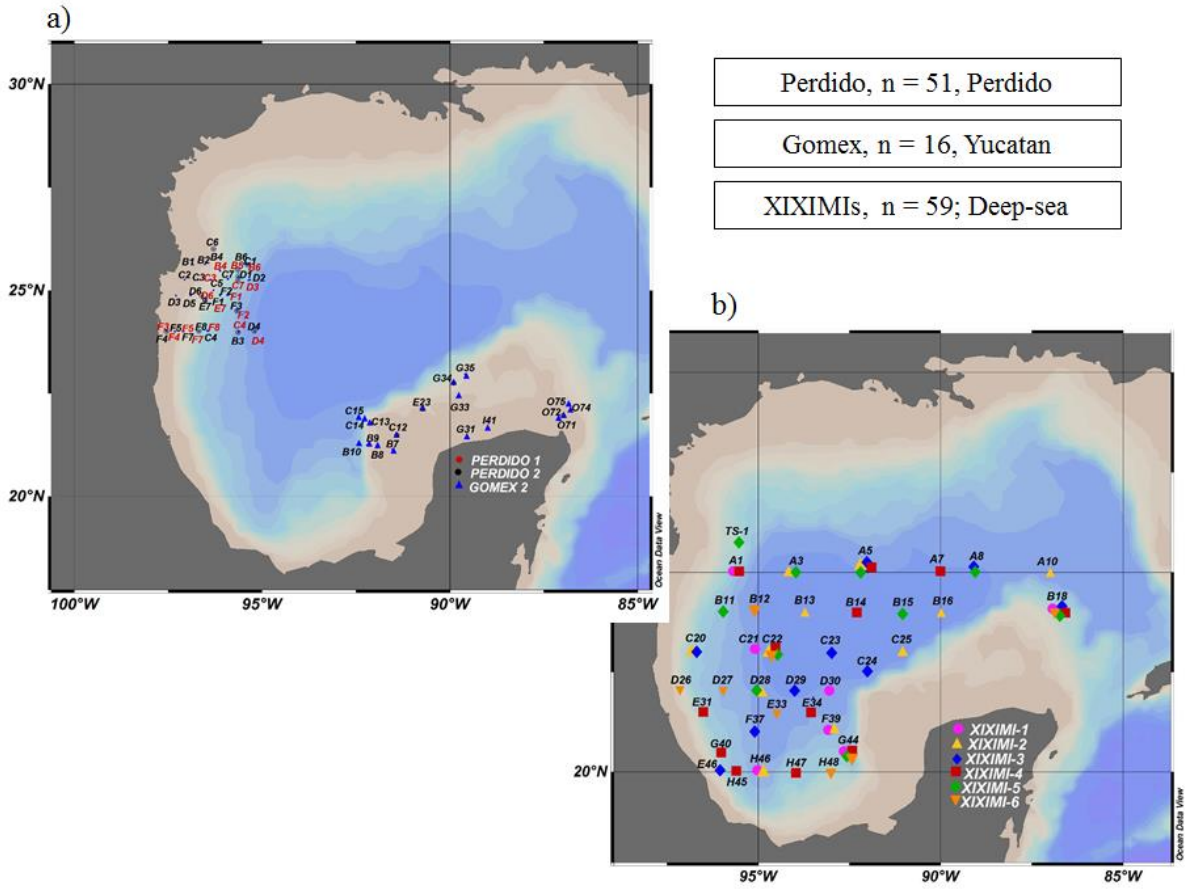

Figure 11. Sampling stations within the Gulf of Mexico. a) sampling stations from Perdido and Yucatan regions, and b) samplings stations from deep-sea.

For the deep sea, samples were taken using 2 devices: (i) box-corer from which cylindrical sediment cores were subsampled with an acrylic core (internal diameter 8.1 cm) and (ii) multicorer device (internal diameter 10 cm). In the Perdido region, the sediment was collected using a 60 x 60 x 40 cm Hessler-Sanders dredger while a Smith-Mcintyre dredger was used in the Yucatan platform; in both campaigns, cylindrical corers were subsampled with a 10 cm diameter core. All sediment cores were frozen at -20°C. Due to sampling constraints, only one core was collected at each station.

3.2.2 DNA extraction

Environmental DNA was extracted from 1.25g (wet weight: in 5 extraction replicates of 0.25g each) of sediment using a modified protocol from the PowerSoil DNA extraction kit (MoBio, Carlsbad, CA, USA). Briefly, in order to increase the amount of DNA recovered, two incubation steps were carried out

overnight and all the DNA was filtered through a single recovery filter (Spin Filter).

3.2.3. Sequencing and bioinformatic pipeline

The amplification, purification and sequencing of the DNA was carried out following the protocol of the "Earth Microbiome Project" for amplicons of the 18S gene (www.earthmicrobiomeproject.org). The V9 region (~260 pb) of the minor subunit of RNA (18S SSU rRNA) was amplified with primers Euk_1389f and Euk_1510r. Sequencing of amplicons was performed on the Illumina HiSeq 2500 platform for 250 bp reads in paired-end sequencing.

After demultiplexing, a table of Sequence Variants was created, analogous to the classic OTU table, following the pipeline DADA2 1.2 implemented in QIIME2. Briefly, the forward and reverse reads were truncated at 200 base pairs based on the quality profiles and the reads were grouped into unique SVs (Callahan et al. 2017). The final SVs in all samples were inferred using a custom parametric error model for each data set. The forward and reverse reads were then merged and a sequence table was constructed with a count of each SV per sample. The DADA2 pipeline fuses the sequences (fordward + reverse), eliminates noisy sequences, eliminates chimeras and infers the sequences of each sample (Callahan et al. 2016).

The taxonomic classification of the SVs was carried out using the BLAST algorithm for each SV, against the SILVA 128 18S SSU rRNA database with the assign-taxonomy_with_BLAST.py script. The taxonomic classification was carried out at the level of phylum, family and species, with consensus BLAST identity percentages higher than 90, 93 and 97%, respectively. These thresholds were chosen based on literature examining simulated communities of benthic metazoans (Brown et al. 2015; Holovachov 2016). Before ecological analyzes, all SVs of non-metazoan organisms were eliminated from the SV table.

3.2.4 Ecological analyses

For all ecological analyzes the continental shelf in the Perdido region was considered up to 200m deep and the sites located at greater depths were considered as continental slope. To answer the study questions we first assessed the structures of the communities in the 4 regions from three perspectives: (i) proportion of the major taxonomic groups, (ii) similarity between the community structures and (iii)

phylogenetic relationships. The last two were evaluated at SVs level.

First, a normalization of the number of reads was performed for all the samples in the SVs table. This standardization was done with the Qiime diversity core-metrics-phylogenetic script in QIIME2, which calculates a set of diversity measures (phylogenetic and non-phylogenetic) from the "feature table".

The similarity of the meiofaunal communities among the 4 regions of the GoM at the level of major taxonomic groups was evaluated with the analysis of similarity (ANOSIM) with "geographic region" as a fixed factor. The similarity of the 4 regions considering the whole community at SVs level was evaluated through a canonical analysis of principal components (CAP) (Anderson and Willis 2003) according to the proportion of each of the SVs as well as to their presence/absence using the Bray-Curtis and Jaccard indexes, respectively. Significance was evaluated using the software PRIMER 6 and PERMANOVA + (Anderson et al. 2008). Because the 4 regionsof the GoM cover different depths, to assess the effect of this factor on meiofaunal communities, a Mantel test ("RELATE") with 4,999 permutations based on distance matrix of depth and community composition (Jaccard) was performed using PRIMER.

In order to evaluate if phylogenetic distances between sequences are greater within or between the 4 regions of the GoM, the UniFraq method was used for all the SVs. This method allows to calculate the differences between microbial communities based on phylogenetic information (Lozupone and Knight 2005). It can be used to determine if one community is significantly different from another by comparing many communities simultaneously using grouping and ordination techniques. The distances calculated with UniFrac are based on two approaches: (i) unweighted, which considers only the presence/absence of the sequences or (ii) weighted, which considers the sum of the counts of the sequences. The distances between communities were also evaluated through CAP analysis and its significance through ANOSIM. To assess the effect of depth of seafloor on phylogenetic relations among all SVs, a Mantel test was performed as previously described.

To assess dispersal among communities, the PERMDISP routine was used with all the SVs. The result of this analysis was used to evaluate if the spatial structure of the meiofaunal community was homogeneous throughout the Gulf or if there are differences between the 3 regions. For this analysis, the average dissimilarity was used as an indicator of multivariate dispersal (i.e., β diversity; Anderson et al. 2006; Anderson et al. 2011). This analysis infers the existence of dispersal if no significant differences are found among GoM regions.

3.3 Results

3.3.1 Sequencing

The total number of reads product of the sequencing was 9,070,545 which was reduced to 4,500,094 grouped in 15,933 SVs after the quality control and the elimination of chimaeras with DADA2. Of these reads, 947,033 correspond to metazoans among which 437,416 belonged to meiofaunal taxa and were grouped into a total of 3,439 SVs. After the normalization of the number of sequences, 8 samples possessing insufficient reads were eliminated for consecutive analyzes (2 from Yucatan, 2 from Perdido and 4 from deep-sea); therefore, all analyzes were performed with 120 sampling stations.

3.3.2 Comparison of the 3 geographic areas

In total 12 large groups were found throughout the GoM, of which Nematoda was dominant in Perdido and the deep sea whereas Annelida dominated in Yucatan (Figure 12). In the Perdido region it is possible to identify different patterns between the two cruises, which reflect the depths covered in each of them, having in Perdido 1 greater coverage of deep sediments (more than 65% > 1000m deep) compared to Perdido 2 (less than 45% > 1000m depth – App 4). This cruise has more similarity with the deep sea community. The similarity analysis revealed significant differences among community structures of geographic regions (R Global = 0.166, $p < 0.05$) except between Perdido (Cruise 1) and the deep sea.

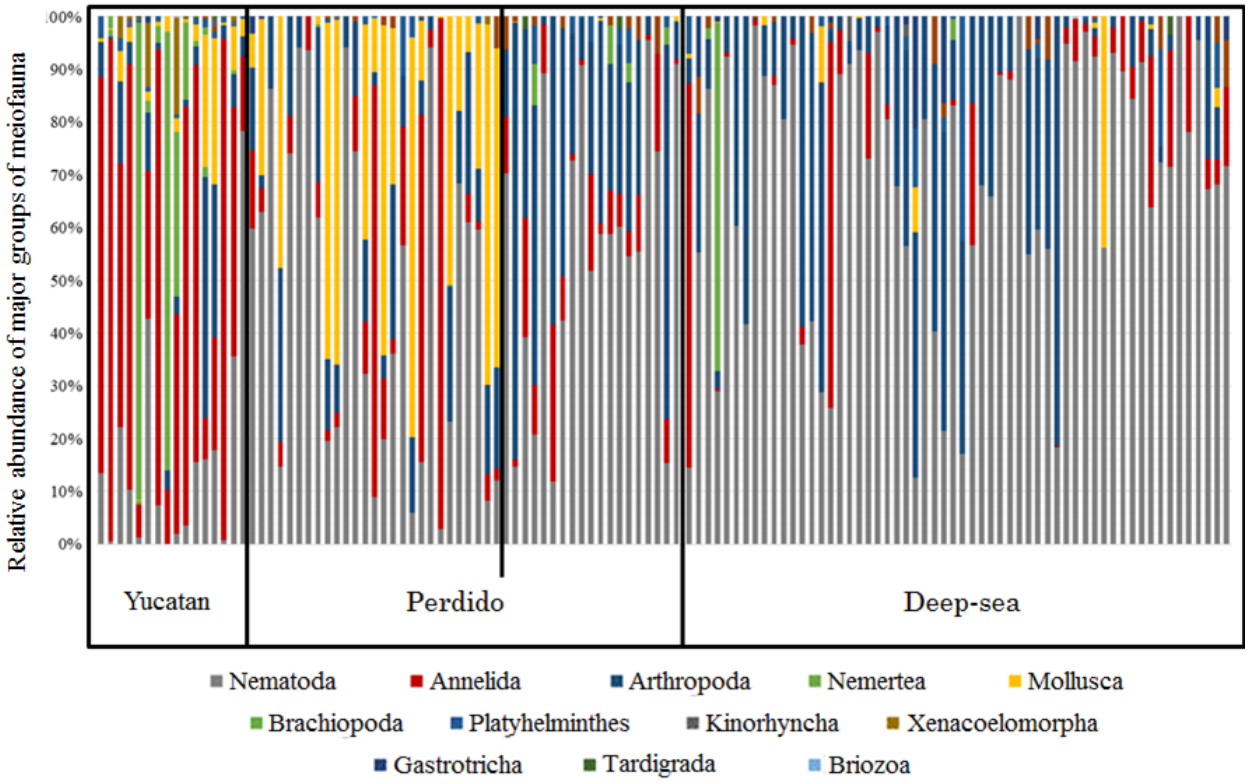

Figure 12. Meiofaunal major taxonomic groups found at each geographic region in the Gulf of Mexico.

CAP analysis revealed significant differences among the community structures of the gulf regions for the Bray-Curtis and Jaccard indices (Global R = 0.597, $p < 0.05$; Global R = 0.272, $p < 0.05$, respectively, Figure 13a and b), except for northwestern shelf and slope regions (R = 0.013, $p > 0.05$; R = 0.025, $p > 0.05$, respectively). This indicates that the two regions from Perdido harbor a meiofaunal community distinct from those of Yucatán and the deep-sea, both in their quantitative structure (considering the number of sequences found - Bray-Curtis index) and in their taxonomic list (presence/absence - Jaccard index). The Mantel test revealed a significant correlation between community composition (presence/absence) and depth of seafloor although the correlation was not strong ($r = 0.24$, $p < 0.05$).

The differences among communities from the geographical regions were also manifested in their phylogenetic relationships and follow the same pattern as quantitative and presence/absence results. The CAP analysis based on the unweighted UniFrac indicated a significant separation among the regions, considering both regions of Perdido as one (Global R = 0.186, $p < 0.05$, Figure 13c). This result suggests that there are ecological processes within each area that have allowed the co-evolution of these

communities. On the other hand, the CAP analysis based on the weighted UniFrac did not reveal significant differences (Global R = -0.003, $p > 0.1$), which suggests that the more abundant SVs are also distributed in the 3 geographical areas of the GoM. As for the community composition, the Mantel test showed a significant correlation between phylogenetic distances and depth ($r = 0.138$, $p < 0.05$).

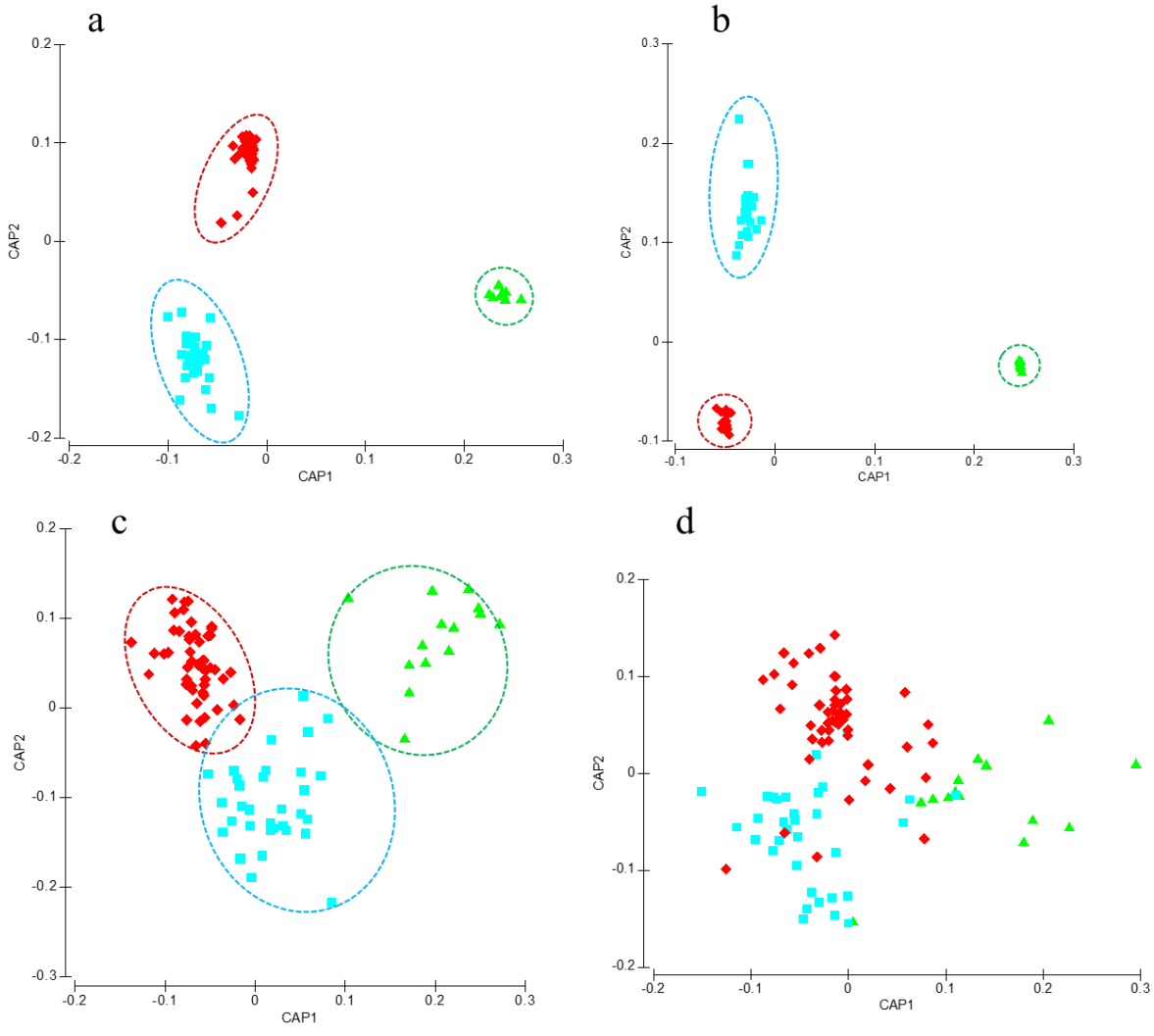

Figure 13. CAP analysis of communities of each geographic region into the Gulf of Mexico. a) Bray-Curtis index, b) Jaccard index based on presence/absence, c) unweighted UniFrac and d) weighted UniFrac. Green triangles: Yucatan shelf, light blue squares: Norwestern shelf, blue inverted triangles: Northwestern slope and red diamonds: Deep-sea.

3.3.3 Dispersal

The PERMDISP analysis for the community revealed significant differences between the GoM

regions according to the taxonomic list (Jaccard) ($F = 27.62$, $p < 0.01$); the differences were found between the deep sea and Yucatan ($t = 5.61$, $p > 0.01$) on the one hand, and the deep sea and northwestern shelf and slope, on the other ($t = 7.87$, $p > 0.001$; $t = 7.27$, $p > 0.001$ respectively) (Figure 14), but not between Yucatán and Perdido.

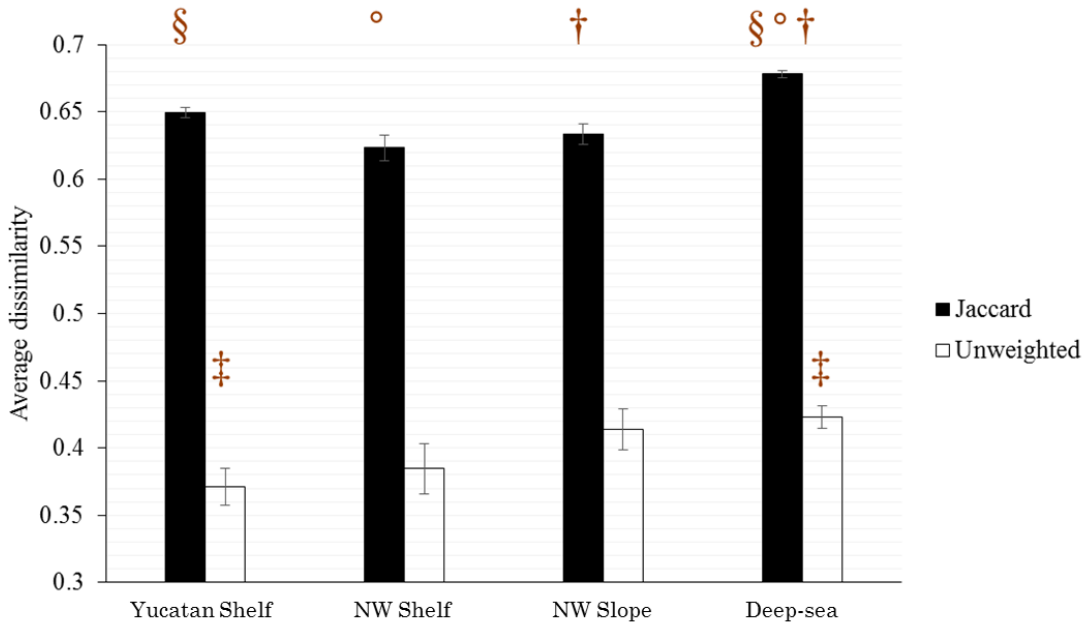

Figure 14. Multivariate dispersion index (PERMDISP) of the communities of the 3 geographic areas in the Gulf of Mexico. Same symbols indicate significant differences.

This suggests that there are shared SVs between the Yucatán and Perdido regions possibly by passive dispersal and/or because the sites of both continental shelves are at the same depth (71.65m $\pm$ 40.25 and 77.34m $\pm$ 25.98 for Yucatán and Perdido shelf respectively). On the other hand, the same analysis based on phylogenetic distances also revealed significant differences ($F = 3.21$, $p < 0.05$) between Yucatan and the deep-sea, which indicates that these two regions have different evolutionary histories. Moreover, the SVs found in Yucatán are genetically similar to Perdido ($t = 0.58$, $p = 0.62$ for NW shelf and $t = 1.91$, $p = 0.09$ for NW slope), which is consistent with the Jaccard result, but also, the SVs of Perdido and the deep-sea are similar ($t = 1.90$, $p = 0.16$ for NW shelf and $t = 0.55$, $p = 0.62$ for NW slope), which suggests that, although there are low levels of within-region variation (compared to among them), and the communities of each geographic region are particular, the Perdido region is an intermediate evolutionary region between Yucatan and the deep sea, besides it suggests that lineages from these two

geographic regions have not yet significantly diverged from Perdido.

3.4 Discussion

3.4.1 Environments

Among all the reported relationships of the marine meiofauna and the environment, the depth of the seafloor is a consistently influential factor in the structure of the benthos, in addition to the sedimentary characteristics. It has been described for oceanic environments that the abundance and community structure of the meiofauna varies in response to the decrease of the exported particulate organic carbon at increasing depths (Giere 2009; Bik et al. 2012; Bianchelli et al. 2013; Bianchelli et al. 2015; Gambi and Danovaro 2016).

Our observations indicate that the structure of the meiofauna differs among the regions of the GoM, the wide geographic coverage of the sampling within the GoM suggests that differences between geographic areas play an important role in the community structures. Although the dispersal of the data between regions is greater than within them, the large scatter of the observations in the Perdido region could be associated to the fact that this region had the greatest bathymetric amplitude between the sampling stations (App 4.1, Figure 13a and b). Sites from Perdido covered the continental shelf and slope what is reflected in the wide scatter of the observations, nevertheless, communities from shelf and slope showed a smaller variation between them than compared with the other regions of the GoM. Otherwise, even though there is a correlation between depth of seafloor and community composition (Mantel test results), and sites from Perdido encompass a wide bathymetric gradient, communities within this region were not significantly different, suggesting that a regional scale the northwestern shelf and slope could be considered as a one independent region (Fig 13 and ANOSIM results). Rosli et al., (2018) mention that the greatest variability in the community attributes of the meiofauna, such as structure, diversity and abundance, is generally observed at a regional scale (100 - 10,000 km) and in the bathymetric gradient (Rosli et al. 2018).

The geographic areas analyzed in this investigation represent very different environments within the Gulf of Mexico. The depth of each of them (App 4), sediment type and the amount of organic matter coming from the surface allow these environments to shelter different biological communities (Bouma

1972; Martin and Bouma 1978; Pica-Granados et al. 1991; Escobar et al. 1997; Ward and Tunnell 2017).

It has been described that differences in the abundance of the meiofauna between regions of the ocean are often associated with differences in productivity regimes (Fonseca and Soltwedel 2009; Gambi et al. 2014). The availability of food in the sediment is related to the flow of organic carbon from the surface of the ocean, which in turn has an effect on the abundance of the meiofauna (Ingels et al. 2009). In this regard, our results shown that there is a bathymetric signal on community structure (quantitative and compositional) that could be related to the input of organic matter from surface waters. Nevertheless, the differences among regions based on ANOSIM analysis could be associated with environmental differences, therefore, it is difficult to suggest the relative importance of depth with respect to the particular environmental variables of each region not considered here. Furthermore, there is a clear but not significant separation between communities from northwestern shelf and slope and that separation could be given by a narrow range of environmental variability compared with the one that exist with Yucatan and the deep sea. In this regard, a research conducted on free-living marine nematodes sampled on the shelf break (300-400m) and upper slope (1000m) of the western Iberian margin to assess the influence of environmental drivers on spatial variability of nematofauna showed that the higher diversity and variability in community structure at the shelf break compared with the upper slope was related to food availability and sediment heterogeneity. Moreover, community differences were more pronounced between shelf and slope than within them, nevertheless this low variability was explained by environmental changes. They concluded that changes in community structure are influenced by environmental factors rather that spatial differences (Lins et al. 2017).

Bik and coworkers (2012) evaluated microbial eukaryotic communities (protists, fungi, nematodes, among other groups) in a bathymetric gradient and between ocean basins (Pacific and Atlantic) and they identified a low genetic divergence between geographically remote sites, which they attributed to a short coalescence time between deep sea regions or at low evolutionary rates at these depths; however, the phylogenetic differences between shallow and deep sites of the same basin were much greater.

Our results indicate that the communities from Yucatan and deep-sea differ significantly in the phylogenetic distances between them, but not with the Perdido region suggesting that the coalescence time between Yucatan-Perdido and deep-sea-Perdido has not been long enough to produce a divergence between their lineages, a similar pattern to that reported by Bik et al. (2012) between Pacific and Atlantic ocean basins. This result also suggests that it is not possible to elucidate a bathymetric effect on meiofaunal phylogenetic relationships at habitat scale but it is possible at regional scale. On the other

hand, the deep-sea sampling stations are separated from each other by up to 1000 km, however the genetic distance between 18S sequences is lower compared to those from Perdido and Yucatán regions (Figure 13c), which could suggest that the deep-sea is a much more stable environment than the other regions, allowing a slower rate of meiofaunal divergence. For marine habitats, it has already been described that the vertical gradient limits the distribution of the species (Aldea et al. 2008) apparently much more than the horizontal geographical distance (Pawlowski et al. 2007), what is concordant with the fact that the geographic regions analyzed here differ among them in the depth of water column (App 4), particularly the differences between Yucatan and deep-sea.

It has been proposed that the deep sea has a static nature, without much variability and that this condition could allow rates of molecular evolution to be slower. However, studies have shown that the deep sea is a very dynamic environment with particularities from geological environments to biological processes that make it an environment very different from other marine ecosystems (Ramirez-Llodra et al. 2010; Danovaro et al. 2014). Sediment heterogeneity (Zeppilli et al. 2016) and the amount of organic carbon (Baguley et al. 2006) have been found to influence meiofauna biodiversity; moreover, community structures can be defined by local environmental characteristics (Cisterna-Céliz et al. 2018). However, results reported here suggest that the deep sea dynamics of the GoM are slower than in the shallower Yucatan and Perdido regions. In the Yucatan region, during intense wind events known as "Nortes" the speed of the current along the coast is very high, which enhances the mix between the coast and the deeper shelf, which in turn plays an important role in the transport of sediment along the Yucatan platform (Torres-Freyermuth et al. 2017). On the other hand, the Perdido region is characterized by a narrow continental margin and an abrupt slope where the "Cordilleras Mexicanas" are found, which are parallel foldings to the coastline and which act as a continental sediment barriers. The region is also under the influence of surface hydrographic dynamics, particularly of the mesoscale rings released by the Loop current, which generate a high primary productivity by upwelling in the continental shelf break; moreover, a layer of minimum oxygen zone has been identified in the upper slope (Vidal et al. 1994; Escobar et al. 1997; Escobar-briones et al. 1999). Our results support our working hypothesis, since each of these three environments of the gulf harbor differing meiofaunal communities.

3.4.2 Dispersal

Meiofauna has been described as a ubiquitous ecological group despite having a low dispersal

potential due to the lack of a larval stage in its life cycle (Giere 2009). It has been described that this cosmopolitan distribution is due to the presence of cryptic speciation which has been proposed for some coastal and continental shelf taxa (Derycke et al. 2007; Derycke et al. 2008; Giere 2009; Hauquier et al. 2017).

Our results suggest that there is dispersal between Yucatan and Perdido (Figure 14 – Jaccard) but that is not enough to influence community structures (Figure 13a and b). For the meiofauna, the investigations that evaluate dispersal present contrasting results. A low level of endemism with high interchange between shallow and deep sea habitats has been reported for enoplid nematodes (Bik et al. 2010). Besides, for deep-sea nematodes it has been described that the dispersal potential is low, alluding to the characteristics of life history; however, the dispersal capacity in this group is still unsuspected (Lambshead and Boucher 2003). On the other hand, the similarity between Yucatan and Perdido could be related to the fact that the shallow samples of Perdido shelf are located at the same depth of Yucatan (App 4) and the meiofaunal organisms could be adapted to this environment.

The phylogenetic distances among the SVs of the regions of the Gulf of Mexico suggest a similarity between Perdido and the deep-sea (Figure 14 – unweighted UniFrac). The lack of significant phylogenetic differences between these two regions and the dispersal between them inferred by the Jaccard index, suggests that there is passive dispersal among the communities of these regions and that the lineages have not yet diverged. A recent investigation conducted in the Southern ocean continental shelf sediments, revealed that horizontal and spatial structuring was found in response to local environmental conditions among sites separated from 15km to 2300km, in combination with dispersal limitation in nematodes (Hauquier et al. 2018) what is concordant with the results found in our research. Nevertheless, in some cases, molecular studies confirmed the existence of large-scale distribution despite lack of active means of dispersal, and others reveal a more restricted distribution related with low dispersal potential (Curini-Galletti et al. 2012; Casu et al. 2014).

One of the most broadly discussed hypothesis of the biodiversity of small organisms is Baas-Becking hypothesis “everything is everywhere, but the environment selects” (Baas-Becking 1934). This hypothesis has been tested on meiofauna through morphological and molecular methods and the results indicates that there are geological and ecological processes that act as barriers of dispersal and/or gene flow in marine environments (Bik et al. 2012; Leasi et al. 2016; Randsø et al. 2018). Our results support this hypothesis since we were able to find different communities, slow dispersal and our results suggest slow coalescence time among lineages from geographic regions within the Gulf.

Therefore, it is possible to suggest that dispersal does not play an active role as a mechanism in the structure of the communities of these three regions of the Gulf of Mexico.

3.5 Conclusion

The Gulf of Mexico represents a very important ocean basin to evaluate the effect of the environment on the structure of biological communities. In this research it is possible to observe that the bathymetric differences of each region and its particular environmental characteristics have a significant effect on meiofaunal communities, moreover they have an influence on phylogenetic relations and that dispersal does not play an active role in structuring these communities.

Chapter 4. Conclusions

Meiofauna is one of the least studied ecological groups and represents an important pillar in the ecology of the communities associated to marine sediments, not only in the interactions between their constituent taxa, but also between them and the macro and microfauna.

In the present research we were able to learn about the abundance and distribution patterns of meiofauna in sediments from the Gulf of Mexico under morphological and molecular approaches, and relate them to environmental characteristics. The results of our research allow us to propose some conclusions:

1.- The abundance of meiofauna of deep-sea sediments from GoM is influenced by environmental variability of the Gulf. For instance the abundance decreases with increasing seafloor depth and with decreasing percentage of sand in the sediments. This indicates that the amplitude of environmental variability at depths below of 1500m is high enough to influence this community attribute.

2.- Functionally, deep water nematofauna is dominated by bacterivores in the GoM. This result is consistent with the poor primary productivity of surface waters, the small amount of particulate organic carbon exported to the seafloor, and with values the abundance and availability of bacterial communities.

3.- Functional structure of nematofauna does not change among different geographic sites of the deep-sea sediments of the GoM. It suggests that this community attribute is stable despite the fact that the communities are composed of different nematode genera.

4.- The nematofauna is composed of an admixture of colonizer and persister genera throughout the GoM; nevertheless, the most abundant functional group (bacterivores) is composed mainly by persister genera. This result suggests the existence of environmental perturbations affecting communities but its influence is not the same on all functional groups.

5.- Phylogenetically, the meiofauna of the geographic region of Perdido is more closely related to Yucatan and deep-sea, than these two regions are to each other. Thereby it is possible to suggest that Perdido acts as an intermediate evolutionary region between Yucatan and deep-sea and that the lineages of these two regions has not yet diverged from Perdido.

6.- Dispersal is not large enough to influence meiofaunal community structure but the variability in environmental characteristics is. It is possible for us to suggest that dispersal among patches from deep-sea is limited and much more among geographic areas, and the structures of communities respond to both, habitat and regional environmental characteristics.

7.- Based on the wide spatial coverage of this research, our results can be considered as baseline of meiofauna within the Gulf of Mexico. We were able to describe meiofaunal community at a large scale within the GoM and it is the first research in the Mexican exclusive economic zone that incorporates a large number of samples and in such a wide geographic area.

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Appendix 1

Abundance of each major taxon of meiobenthos and total abundance (ind $10cm^{-2}$)

Cruise	Sampling Station	Nematoda	Copepoda	Ostracoda	Polychaeta	Platyhelminthes	Gastrotricha	Tardigrada	Tanaidacea	Syncarida	Hydrozoa
XIXIMI-1	A1	435.15	15.72	1.32	0.42	9.18	0.00	0.00	0.00	0.00	0.00
	B18	299.70	8.74	3.92	0.45	0.00	0.00	0.00	0.00	0.00	0.00
	C21	144.61	6.99	0.00	0.00	2.19	0.00	0.00	0.00	0.00	0.00
	D30	163.83	4.37	1.32	0.45	6.11	0.00	0.00	0.00	0.00	0.00
	F39	237.22	7.86	2.62	0.45	12.23	1.32	0.00	0.00	0.00	0.00
	G44	245.10	3.93	1.75	0.43	11.79	0.43	0.00	0.00	0.00	0.00
	H46	301.01	6.12	1.75	4.79	4.37	0.00	0.00	0.00	0.00	0.00
XIXIMI-2	A3	178.63	15.13	0.00	0.00	5.04	0.00	0.00	0.00	0.00	0.00
	A5	220.13	22.30	0.19	0.19	28.70	0.00	0.19	0.00	0.00	0.00
	A10	109.78	7.18	0.00	0.39	11.44	0.00	0.00	0.00	0.00	0.00
	B13	142.94	6.59	0.00	0.39	8.15	0.00	0.00	0.00	0.00	0.00
	B16	248.64	20.36	0.39	0.39	9.70	0.19	0.19	0.00	0.00	0.00
	C20	167.18	12.99	0.19	0.39	5.82	0.00	0.00	0.00	0.00	0.00
	C22	128.01	12.22	0.00	0.19	8.53	0.19	0.00	0.00	0.00	0.00
	C25	179.79	11.06	0.00	0.19	12.02	0.19	0.00	0.00	0.00	0.00
	D28	196.47	11.25	0.00	0.00	12.41	0.00	0.00	0.00	0.00	0.00
	F39	251.16	19.20	0.78	0.39	4.07	0.00	0.00	0.00	0.00	0.00
	H46	291.31	21.92	0.39	0.00	7.56	0.19	0.00	0.19	0.00	0.00
XIXIMI-3	A5	97.75	7.37	0.00	0.39	7.76	0.00	0.00	0.00	0.19	0.19
	A8	112.30	7.56	0.00	0.97	14.93	0.00	0.19	0.00	0.19	0.00
	B18	206.36	23.66	0.00	1.36	3.88	0.58	1.36	0.00	0.19	0.00
	C20	102.79	12.02	0.00	0.00	12.22	0.19	0.19	0.19	0.19	0.00
	C23	59.35	2.52	0.58	0.39	19.01	0.00	0.00	0.00	0.00	0.19
	C24	185.03	13.77	0.00	0.78	19.01	0.00	0.00	0.00	0.19	0.00
	D29	81.26	3.49	0.00	0.00	20.56	0.00	0.00	0.00	0.00	0.19
	E46	169.71	21.92	0.00	0.39	5.82	0.00	0.00	0.00	0.19	0.00
	F37	111.33	12.80	0.00	1.36	24.44	0.00	0.00	0.00	0.19	0.19

Cruise	Nemertea	Isopoda	Asteroidea	Kinorhyncha	Sipuncula	Acari	Oligochaeta	Loricifera	Total Abundance
XIXIMI-1	0.00	0.00	0.00	0.00	0.00	0.00	8.75	0.00	470.534
	0.00	0.00	0.00	0.00	0.00	0.00	6.12	0.00	318.932
	0.00	0.00	0.00	0.00	0.00	0.00	1.32	0.00	155.113
	0.00	0.00	0.00	0.00	0.00	0.00	2.19	0.00	178.270
	0.00	0.00	0.00	0.00	0.00	0.00	3.07	0.00	264.784
	0.00	0.00	0.00	0.00	0.00	0.00	2.18	0.00	265.605
	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.00	323.705
XIXIMI-2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	198.798
	0.19	0.00	0.39	0.19	0.00	0.00	0.19	0.00	272.692
	0.00	0.00	3.10	0.00	0.00	0.00	0.00	0.00	131.885
	0.39	0.00	0.00	0.19	0.00	0.00	0.00	0.00	158.650
	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	280.062
	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	186.773
	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	149.341
	0.58	0.00	0.19	0.00	0.00	0.00	0.00	0.00	204.034
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	220.132
	0.00	0.00	0.19	0.00	0.00	0.00	0.19	0.00	275.989
	0.58	0.00	0.00	0.58	0.00	0.00	0.00	0.00	322.731
XIXIMI-3	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	113.848
	0.19	0.19	0.00	0.00	0.00	0.00	0.00	0.00	136.540
	0.00	0.00	0.97	0.00	0.00	0.00	0.00	0.19	238.557
	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	128.200
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	82.040
	0.58	0.00	0.00	0.00	0.19	0.58	0.00	0.00	220.126
	0.19	0.00	0.00	0.19	0.00	0.00	0.00	0.00	105.896
	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.00	198.412
	1.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	152.056

Appendix 2

Detailed information of the environmental variables of each sampling station of XIXIMI-1, 2 and 3. IC: inorganic carbon, TOC: total organic carbon, C/N: carbon/nitrogen ratio.

Cruise	Sampling station	Depth (m)	Latitude °N	Longitude °W	Sediment classification	%Clay (< 4 µm)	%Silt (4- 62 µm)	%Sand (62–2 mm)
XIXIMI-1	A1	2,416	25.008	-95.601	very fine silt	25	74	1
	B18	1,233	23.988	-86.758	very coarse silt	8	58	34
	C21	3,569	23.008	-95.005	fine silt	30	63	7
	D30	3,297	21.991	-93.009	fine silt	25	72	3
	F39	2,549	21.007	-92.998	fine silt	27	71	2
	G44	2,464	20.496	-92.675	fine silt	24	72	4
	H46	2,758	20.011	-95.005	fine silt	18	74	8
XIXIMI-2	A3	3,700	24.990	-93.982	fine silt	19	65	16
	A5	3,521	25.006	-91.986	coarse silt	16	66	18
	A10	3,341	25.000	-87.010	very coarse silt	9	34	56
	B13	3,739	24.003	-93.725	fine silt	22	79	0
	B16	3,628	23.989	-89.994	coarse silt	14	60	26
	C20	1,791	23.011	-96.709	fine silt	18	72	10
	C22	3,727	23.000	-94.520	fine silt	20	67	13
	C25	3,714	23.017	-91.013	fine silt	17	82	0
	D28	3,367	22.011	-95.002	fine silt	19	68	13
	F39	2,246	21.003	-93.026	coarse silt	11	67	22
	H46	2,756	20.017	-95.007	fine silt	18	81	1
XIXIMI-3	A5	3,484	25.028	-92.047	coarse silt	-	-	-
	A8	3,469	25.010	-88.983	coarse silt	-	-	-
	B18	1,240	24.076	-86.821	very coarse silt	-	-	-
	C20	1,937	23.029	-96.694	fine silt	-	-	-
	C23	3,715	22.998	-92.985	fine silt	-	-	-
	C24	3,559	22.489	-92.018	fine silt	-	-	-
	D29	3,569	21.997	-94.004	fine silt	-	-	-
	E46	1,598	20.029	-96.018	fine silt	-	-	-
	F37	3,055	21.013	-95.086	fine silt	-	-	-

Cruise	IC	TOC	C/N	Oxygen
XIXIMI-1	20.93	1.44	6.49	4.94
	75.99	0.26	7.82	4.4
	36.65	1.15	6.32	3.88
	32.08	1.38	6.33	4.01
	28.09	1.36	8.24	4.93
	24.79	1.54	14.20	3.98
	19.89	1.11	8.13	4.93
XIXIMI-2	28.25	1.51	5.35	4.67
	33.26	1.21	6.19	4.76
	48.71	1.12	5.05	4.78
	34.73	1.43	6.91	4.66
	51.94	1.45	8.29	4.66
	21.18	1.31	6.11	4.1
	36.65	1.15	6.32	4.66
	48.91	1.64	10.80	4.67
	32.26	1.46	5.90	4.09
	28.09	1.36	8.24	4.73
	19.89	1.11	8.13	4.71
XIXIMI-3	33.26	1.21	6.19	4.71
	33.28	1.05	8.25	4.75
	75.99	0.26	7.82	4.36
	21.18	1.31	6.11	4.7
	35.31	0.92	7.22	4.82
	41.20	1.27	7.03	3.94
	31.80	1.00	7.90	3.9
	25.21	1.00	8.32	4.03
	28.00	1.05	8.38	4.81

Appendix 3

Nematode families and genera found in XIXIMI-1. Results in ind $10cm^{-2}$.

Family	Genera	Trophic Group	c-p value	A1	B18	C22	D30	F39	G44	H46	Total
Aegialoalaimidae	*Aegialoalaimus*	1A	2	7.77	0	0	7.77	15.53	15.53	0	**46.60**
	Diplopeltoides	-	4	23.30	0	0	0	0	0	0	**23.30**
Anoplostomatidae	*Anoplostoma*	1B	2	0	0	0	0	7.77	7.77	0	**15.53**
Anticomidae	*Anticoma*	1A	2	0	7.77	0	0	0	0	0	**7.77**
	Cephalanticoma	2A	2	0	0	7.77	0	0	0	0	**7.77**
Aphalenchoididae	*Aphelenchoides*	-	2	0	7.77	46.60	46.60	124.27	93.20	62.14	**380.58**
Axonolaimidae	*Axonolaimus*	1B	2	7.77	7.77	0	7.77	0	0	0	**23.30**
Ceramonematidae	*Metadasynemella*	1A	3	15.53	15.53	0	7.77	0	0	0	**38.83**
	Pselionema	1A	3	15.53	15.53	0	15.53	15.53	7.77	15.53	**85.44**
Chromadoridae	*Acantholaimus*	2A	-	31.07	0	0	0	7.77	0	0	**38.83**
	Actinonema	2A	4	0	7.77	0	0	0	0	0	**7.77**
	Endeolophos	-	-	0	0	15.53	0	0	0	0	**15.53**
Comesomatidae	*Hopperia*	2A	2	0	0	0	0	7.77	7.77	0	**15.53**
	Laimella	2A	2	0	7.77	0	0	0	0	0	**7.77**
	Sabatieria	1B	2	7.77	0	7.77	0	0	0	0	**15.53**
Cyatholaimidae	*Acanthonchus*	-	3	7.77	0	0	0	0	0	0	**7.77**
	Longicyatholaimus	2A	3	7.77	0	0	0	0	7.77	7.77	**23.30**
	Marylynnia	2A	3	15.53	0	7.77	15.53	7.77	7.77	7.77	**62.14**
	Minolaimus	-	3	0	0	7.77	0	0	0	0	**7.77**
	Paralongicyatholaimus	2A	3	7.77	0	0	15.53	7.77	7.77	0	**38.83**
	Praeacanthonchus	2A	3	15.53	31.07	0	0	0	0	7.77	**54.37**
Desmodoridae	*Desmodora*	2A	3	15.53	0	0	0	0	0	7.77	**23.30**
	Molgolaimus	1A	3	31.07	0	0	15.53	23.30	31.07	15.53	**116.50**
Desmoscolecidae	*Calligyrus*	1A	4	0	0	0	0	0	0	7.77	**7.77**
	Desmoscolex	1A	4	46.60	7.77	7.77	7.77	38.83	23.30	46.60	**178.64**
	Greeffiella	1A	4	0	15.53	0	15.53	15.53	0	15.53	**62.14**
	Pareudesmoscolex	1A	4	7.77	7.77	15.53	15.53	15.53	15.53	0	**77.67**
Diplopeltidae	*Campylaimus*	1B	3	7.77	0	0	0	0	0	7.77	**15.53**
	Southerniella	1A	3	31.07	7.77	7.77	0	0	0	7.77	**54.37**
	Diplopeltula	-	3	31.07	23.30	0	0	23.30	23.30	0	**100.97**
Enchelidiidae	*Belbolla*	2B	4	7.77	7.77	15.53	7.77	7.77	15.53	0	**62.14**
	Polygastrophora	2B	4	0	0	7.77	0	0	0	0	**7.77**
Epsilonematidae	*Epsilonema*	1A	4	7.77	0	0	0	0	0	0	**7.77**
Thoracostomopsidae	*Enoploides*	-	2	0	7.77	0	0	0	0	0	**7.77**
Haliplectidae	*Setoplectus*	1A	3	0	15.53	0	0	0	0	15.53	**31.07**

Family	Genera	Trophic Group	c-p value	A1	B18	C22	D30	F39	G44	H46	Total
Ironidae	*Syringolaimus*	2B	4	7.77	0	0	0	0	0	0	**7.77**
	Thalassironus	2B	4	0	0	0	0	0	0	7.77	**7.77**
	Trissonchulus	2B	4	7.77	0	0	0	0	0	15.53	**23.30**
Leptolaimidae	*Antomicron*	-	3	15.53	7.77	0	0	0	0	15.53	**38.83**
	Leptolaimoides	1A	3	0	7.77	0	0	0	0	0	**7.77**
	Leptolaimus	1A	2	31.07	15.53	0	0	0	15.53	15.53	**77.67**
	Procamacolaimus	-	3	0	23.30	7.77	0	0	0	0	**31.07**
Leptosomatidae	*Leptosomatum*	-	5	0	7.77	0	0	0	0	0	**7.77**
Linhomoeidae	*Disconema*	1A	3	7.77	0	0	0	0	7.77	7.77	**23.30**
	Metadesmolaimus	1B	3	0	7.77	0	0	0	0	0	**7.77**
	Metalinhomoeus	-	3	0	7.77	0	0	0	0	0	**7.77**
	Terschellingia	1A	3	0	7.77	0	0	0	0	0	**7.77**
Meyliidae	*Gerlachius*	1A	4	0	7.77	0	15.53	7.77	23.30	0	**54.37**
	Meylia	-	-	0	7.77	0	0	0	0	0	**7.77**
Microlaimidae	*Aponema*	1A	3	46.60	31.07	15.53	0	0	0	0	**93.20**
	Calomicrolaimus	2A	3	0	0	0	0	7.77	0	7.77	**15.53**
	Microlaimus	2A	2	54.37	54.37	15.53	15.53	15.53	38.83	15.53	**209.71**
Monhysteridae	*Diplolaimella*	1B	1	31.07	7.77	7.77	7.77	0	0	7.77	**62.14**
	Gammarinema	1B	1	0	7.77	0	0	0	0	0	**7.77**
	Monhystera	1B	1	0	0	0	7.77	7.77	7.767	0	**23.30**
Undefined	Undefined	-	-	0	7.77	7.77	0	0	0	7.77	**23.30**
Oxystominidae	*Halalaimus*	1A	4	46.60	15.53	23.30	23.30	15.53	7.767	38.83	**170.87**
	Nemanema	1A	4	0	0	0	0	0	0	7.77	**7.77**
	Oxystomina	1A	4	7.77	7.77	0	0	0	0	7.77	**23.30**
	Wieseria	1A	4	0	0	0	0	0	0	15.53	**15.53**
Phanodermatidae	*Crenopharynx*	2A	4	15.53	0	0	0	0	0	7.77	**23.30**
	Phanoderma	2B	4	0	0	0	0	0	0	7.77	**7.77**
Selachinematidae	*Gammanema*	2B	3	7.77	7.77	0	0	0	0	0	**15.53**
	Halichoanolaimus	2B	3	0	7.77	0	0	0	0	0	**7.77**
Sphaerolaimidae	*Metasphaerolaimus*	2B	3	15.53	7.77	0	15.53	7.77	0	23.30	**69.90**
	Sphaerolaimus	2B	3	0	7.77	0	0	0	0	0	**7.77**
Tarvaiidae	*Tarvaia*	1A	-	7.77	0	0	0	0	0	7.77	**15.53**
Xyalidae	*Ammotheristus*	1B	2	0	0	0	0	7.77	15.53	0	**23.30**
	Amphimonhystrella	1B	2	38.83	31.07	0	7.77	7.77	7.77	7.77	**100.97**
	Elzalia	1B	2	15.53	0	0	0	0	0	15.53	**31.07**
	Linhystera	1A	2	0	7.77	0	0	0	0	0	**7.77**

Appendix 4

4.1 Depth and geographic location of sampling stations from Perdido region.

Cruise	Sampling Station	Depth (m)	Latitude ° N	Longitude ° W
Perdido 1	B3	470	25.742	-96.258
	B4	1,074	25.471	-96.119
	B5	1,610	25.493	-95.641
	B6	1,847	25.619	-95.392
	C3	559	25.254	-96.368
	C4	1,100	25.007	-96.296
	C5	1,760	25.273	-95.901
	C6	1,810	25.260	-95.641
	C7	2,808	25.245	-95.361
	D3	472	24.874	-96.611
	D4	800	24.753	-96.509
	D5	1,280	24.875	-96.117
	D6	2,085	24.881	-95.901
	E7	2,812	24.514	-95.680
	F1	49.7	24.002	-97.539
	F2	116	24.009	-97.318
	F3	435	24.001	-97.111
	F4	1,620	24.005	-96.676
	F5	2,000	24.014	-96.433
	F7	2,847.60	24.013	-95.623
	F8	3,437	24.009	-95.194
Perdido 2	B1	50	25.621	-96.836
	B2	93	25.634	-96.517
	B3	498	25.750	-96.253
	B4	989.7	25.486	-96.127
	B5	1412.2	25.644	-95.489
	B6	1789	25.636	-95.414
	C1	46	25.252	-97.059
	C2	102	25.255	-96.702
	C3	520	25.255	-96.352
	C4	291.6	26.004	-96.287
	C5	1507.8	25.277	-95.922
	C6	1998	25.343	-95.629
	C7	2891	25.254	-95.320
	D1	44	24.870	-97.293
	D2	105	24.872	-96.899
	D3	490	24.873	-96.599
	D4	812	24.773	-96.511
	D5	1270	24.898	-96.124
	D6	2109.5	24.884	-95.927
	E7	2931	24.501	-95.671
	F1	47.17	24.019	-97.552
	F2	87.4	24.001	-97.316
	F3	490	24.008	-97.084
	F4	1500	24.012	-96.682
	F5	1918.16	24.019	-96.460
	F7	3034.5	23.976	-95.635
	F8	3466	24.010	-95.201

4.2 Depth and geographic location of sampling stations from Yucatan Shelf.

Cruise	Sampling Station	Depth (m)	Latitude ° N	Longitude ° W
Gomex	B7	40	21.144	-91.534
	B8	52	21.189	-91.938
	B9	56.8	21.245	-92.207
	B10	97.3	21.281	-92.393
	C12	44	21.485	-91.409
	C13	54.4	21.782	-92.124
	C14	100.4	21.841	-92.257
	C15	220	21.911	-92.423
	E23	44.5	22.119	-90.731
	G31	16.6	21.410	-89.561
	G33	51	22.393	-89.818
	G34	105	22.964	-89.600
	G35	159	22.746	-89.894
	I41	21.7	21.694	-89.005
	O71	23.1	21.885	-87.089
	O72	25	21.952	-86.989
	O74	81	22.207	-86.843
	O75	123	22.250	-86.809

4.3 Depth and geographic location of sampling stations from deep-sea.

Cruise	Sampling Station	Depth (m)	Latitude ° N	Longitude ° W
XIXIMI-1	A1	2416	25.008	-95.601
	B18	1233	23.988	-86.758
	C22	3569	23.008	-95.005
	D30	3297	21.991	-93.009
	F39	2549	21.007	-92.998
	G44	2464	20.496	-92.675
	H46	2758	20.011	-95.005
XIXIMI-2	A3	3700	24.990	-93.982
	A5	3521	25.006	-91.986
	A10	3341	25.000	-87.010
	B13	3739	24.003	-93.725
	B16	3628	23.989	-89.994
	C20	1791	23.011	-96.709
	C22	3727	23.000	-94.520
	C25	3714	23.017	-91.013
	D28	3367	22.011	-95.002
	F39	2246	21.003	-93.026
	H46	2756	20.017	-95.007
XIXIMI-3	A5	3484	25.028	-92.047
	A8	3469	25.010	-88.983
	B18	1240	24.076	-86.821
	C20	1937	23.029	-96.694
	C23	3715	22.998	-92.985
	C24	3559	22.489	-92.018
	D29	3569	21.997	-94.004
	E46	1598	20.029	-96.018
	F37	3055	21.013	-95.086
XIXIMI-4	A1	2429	25.000	-95.533
	A5	3528	25.000	-92.000
	A7	3534	24.950	-90.000
	B14	3734	24.000	-92.300
	B18	1183	23.900	-86.783
	C22	3721	23.000	-94.550
	C22R	3721	23.000	-94.550
	E31	1549	21.500	-96.517
	E34	3146	21.483	-93.500
	G40	1930	20.483	-95.984
	G44	2470	20.517	-92.617
	H45	2159	19.983	-95.600
	H45R	2159	19.983	-95.600
	H47	1342	20.000	-94.017

Cruise	Sampling Station	Depth (m)	Latitude ° N	Longitude ° W
XIXIMI-5	G44	2353	20.533	-92.517
	H47	1865	20.034	-94.017
	D26	1343	22.017	-97.017
	B11	2298	24.050	-95.934
	TS1	1355	25.733	-95.533
	A3	3685	25.034	-94.000
	A5	3513	25.117	-92.000
	A8	3477	25.117	-89.050
	B18	1242	23.967	-86.717
	B15	3708	23.967	-91.017
	C22	3717	22.983	-94.550
	D28	3721	21.983	-95.050
XIXIMI-6	B12	3508	24.050	-95.117
	B18	1150	24.050	-86.883
	C22	3727	23.000	-94.517
	D26	966	22.017	-97.117
	D27	2722	22.000	-96.000
	E33	3431	21.483	-94.500
	G44	2384	20.500	-92.500
	G44-R	2374	20.500	-92.500
	H48	1201	20.017	-93.017