Metacommunity analysis of meiobenthos of deep-sediments from the Gulf of Mexico

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ABSTRACT

Background

Metacommunity theory is a conceptual framework addressing the interdependence of local interactions and regional processes, especially when communities have no clear boundaries and it is difficult to relate community structure and the environment at different spatial scales.

Methods

To test the applicability of this theory to meiobenthos, twenty-seven deep-sea sediment samples from the Gulf of Mexico were analyzed for meiobenthic and nematode community distribution and structure along with a set of environmental variables.

Results

Spatial and temporal heterogeneity in environmental conditions were found among sampling stations; and some variables, such as depth, inorganic carbon, carbon/nitrogen ratio, oxygen and percentage of sand, proved influential on total community abundance. Nematodes were the dominant meiofaunal group and its abundance highly variable among sites and sampling periods. Nematofauna was dominated by bacterivory, which also possessed the highest maturity index. Environmental characteristics showed a significant relation with community structure, not so the dispersal of nematode genera.

Discussion

In light of our findings we posit that the deep-sea meiobenthos of the Gulf of Mexico may represent a metacommunity following the “species sorting model”. This inference is based on the different

43 taxonomic structures among sampling stations correlating with environmental differences, in the
44 presence of local niche diversification and limited dispersal.
45
46
47 ## Introduction
48
49 A crucial question in ecology is how environmental drivers influence biodiversity patterns within
50 and among communities. Diverse factors have been found to affect the communities inhabiting the
51 interstitial space of marine sediments (i.e. meiofauna). Salinity, temperature and sediment grain
52 size have an effect on intertidal meiofauna, where sediment grain size is probably the most
53 important[1] . On the other hand, deep-water communities are more affected by sediment
54 heterogeneity, productivity, food supply, bottom-water oxygen, deep-sea currents, and
55 catastrophic disturbances[2,3]. Of these variables, it has been shown that depth has an important
56 effect on abundance, diversity, and meiofaunal standing stock[1,2], whereas the other variables have
57 been associated with patterns of horizontal zonation, biodiversity and ecosystem functioning[4,5].
58 Because of its ubiquity, meiofauna is considered a cosmopolitan ecological group[7]; however,
59 because of the limited dispersal capabilities of meiofaunal species, their apparent ubiquity gives
60 rise to the "meiofaunal paradox"[1,6].
61 Meiobenthic taxa are characterized by their short generation time; hence, they have a patchy spatial
62 distribution with densities very difficult to predict, especially for deep-sea communities having
63 been significantly less studied than coastal ones. In this regard, the existence of cryptic taxa has
64 been revealed by genetic analyses in some coastal nematode species; for example, remarkable
65 changes in allele composition among adjacent populations have been shown in the cosmopolitan

nematodes *Geomonhystera disjuncta* and *Pellioditis marina*, revealing metapopulation dynamics[1,7,8].

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[9]. 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[10], 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 sea bed morphology is irregular and sediment type is heterogeneous[5], 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[1,11,12]. 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[13].

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[14]. It is based in 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[15–18]. On the other hand, the index of trophic diversity (ITD)[19], has been used to investigate the functional diversity of nematode communities; therefore, ITD allows testing diversity and ecosystem functioning hypotheses such as the positive correlation

between biodiversity and ecosystem function and stability[20,21], and allows to evaluate hypothesis 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[14,22,23].

Interactions among species result in ecological processes occurring at different spatial scales[24,25], such as colonization and extinction patterns, demography of local communities influenced by flow of organisms from another communities, among others. Hence, the concept of metacommunity has been proposed to study the interaction of different species at a regional scale. A metacommunity[25] 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 null hypothesis for the other three paradigms[25].

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 in 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 and its frequency 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[26–30], defined by Whittaker (1960)[31] 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[30]; nonetheless, β diversity measures species substitution and species loss (or gain) among communities[32].

Here, we study the meiofaunal community structure from the deep Gulf of Mexico (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%[33,34], whilst the sediment of the central and south sections of the abyssal plain have a hemipelagic origin, and are mainly composed of pelagic foraminiferan shells[34] (for a deep environmental description of the GoM see[35,36]).

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 indexes), 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 MS paradigms.

Material and Methods

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, n = 7, November 2010), XIXIMI-2 (X-2, n = 11, June 2012) and XIXIMI-3 (X-3, n = 9, February 2013) cruises. With the aim of sampling most of the GoM, sampling stations were located in different physiographic and sedimentary regions[37,38]. 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. 1).

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) which were preserved in 10% buffered formalin.

Meiofauna extraction

Meiofauna was extracted from the sediment matrix by decantation and flotation with colloidal silica (Ludox ™, specific gravity 1.15g cm^{-3} [39]) followed by sieving through a 1000 µm mesh, and retained on a 45 µm mesh[40]. The process was repeated three times to maximize the number of extracted organisms. Once separated from sediment, organisms replaced in 10% buffered formalin in a final volume of 40ml.

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 were identified to major taxa using a Primo Star microscope (Carl Zeiss) following the descriptions in Giere (2009)[1]. 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[41–43] and the Nemys database (*http://nemys.ugent.be/*). Identified nematodes were classified into four functional

183 groups: 1A selective deposit feeders, 1B non-selective deposit feeders, 2A epistrate or epigrowth
184 feeders and 2B predators/omnivores[19].
185
186 Ecological analyses
187
188 We computed diversity as genus richness (S), equitability (J) and Shannon-Wiener (H') indexes
189 for each sample from X-1. To estimate the life-strategy dominance of the nematode community,
190 each genus was assigned a colonizer-persister (c-p) scores, as detailed in Bongers 1990, 1991,
191 1998[14,22,23]. Subsequently, the maturity index (MI) was computed as the weighted mean of c-p
192 scores: $MI = \Sigma\, \upsilon\,(i) * f\,(i)$, where υ is the c-p value of genus i as given in the Appendix of Bongers
193 et al., 1991,[23] and f (i) is the frequency of that genus. In this way, communities with an MI nearest
194 to 1 will be composed mainly by colonizers and communities with an MI nearest to 5 will be
195 composed mainly by persisters. Nematode functional diversity was estimated using the Index of
196 Trophic Diversity (ITD) as 1 – ITD according to Wieser, 1953[19], where $ITD = \Sigma\, \theta^2$, θ is the
197 relative contribution of each trophic group to total abundance. Values range from 0 (lowest trophic
198 diversity, only one trophic group) to 0.75 (highest trophic diversity, where each of the four trophic
199 groups is equally abundant).
200
201 Environmental analyses
202
203 Granulometric analyses were conducted for each core using a laser particle size analyzer HORIBA
204 LA910. Sediment from the three cruises was classified as (i) very fine silt, (ii) fine silt, (iii) coarse
205 silt, and (iv) very coarse silt. For cruises X-1 and X-2 were determined the % of sand, silt and clay.

206 Total organic and inorganic carbon was determined by LECO combustion techniques, and
207 dissolved oxygen was measured from water at 200m above the sediment.
208
209 Data analyses
210 In order to analyze abundance patterns, we first estimated the total abundance from the aliquots
211 analyzed in the X1 cruise. For this we regressed abundance from the entire sample as a function
212 of abundance estimated from the 25% aliquiots in cruises X2 and X3, and used the linear equation
213 to estimate total abundance for X1 samples.
214 The first step to apply the metacommunity theory is to establish if the environmental variables are
215 spatially heterogeneous and to determine if the environmental variability is related to meiobenthic
216 community. Hence, a Principal Components Analysis (PCA) was conducted using log transformed
217 and normalized data. To relate meiobenthic abundance with environmental variables, Canonical
218 Analysis of Principal Coordinates (CAP) was conducted on meiobenthic abundance using the
219 number of components obtained from PCA. CAP analysis is a constrained ordination analysis that
220 takes into account the correlation structure among the variables in the response data[44] and
221 generates scores that were used in correlation analyses with the total abundance of meiobenthos.
222 Subsequently, to investigate the existence of a temporal and sediment type effects over total
223 abundance for both meiobenthic community and nematofauna, were analyzed through
224 PERMANOVA with time as a first factor (3 levels: 2010, 2012 and 2013) and sediment type as a
225 second factor (4 levels: very fine silt, fine silt, coarse silt and very coarse silt). A posteriori pair-
226 wise tests were performed to identify significant terms. All analyses were carried out using
227 PRIMER 6 & PERMANOVA+ software packages[45].
228
229 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[30]. In this paper we analyze β_{cc} as defined by Colwell & Coddington (1994)[46] (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 and coworkers[32]. Pairwise matrices of β_{-3} and β_{-rich} were correlated to a matrix of pairwise geographic distances to test the effect of spatial separation on community structure. The expressions are as follows Koleff et al. (2003)[30].

$$\beta cc = \beta - 3 + \beta rich \quad (1)$$

and

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

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

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 E15 and E27 are located)[47]. 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[48].

253 Environmental differences among sampling stations

254

255 In order to evaluate if the environmental differences have an effect on nematode communities and
256 identify which metacommunity paradigm may explain our findings, we correlated environmental
257 distance (Euclidean distance) among sampling stations with geographic distance as in β diversity.
258 First, environmental distance including all environmental variables, was correlated with
259 geographic distance among sampling stations, to test for an environmental gradient. Second, to
260 test if the environment differences among sampling stations have an effect on community structure
261 we used the environmental distance among sampling stations calculated from the scores of CAP 1
262 of X-1 CAP analysis to correlate them with β_{cc} diversity. Environmental distance was calculated
263 using PRIMER 6 & PERMANOVA+ software packages[45].

264

265 ## Results

266

267 Meiobenthic community

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269 As expected, the regression between abundance from entire samples and from 25% aliquots of X-
270 2 and X-3 was linear, significant ($R^2 = 0.83$; $p < 0.01$, 95%, Fig. 2), and was used to estimate the
271 abundances for the total of X-1 samples for subsequent analyses.
272 We were able to find 18 major taxa among all organisms (X-1:7; X-2: 12; X-3: 17): nematoda,
273 copepoda, ostracoda, oligochaeta, polychaeta, turbellaria, gastrotricha, tardigrada, loricifera,
274 syncarida, tanaidacea, hidrozoa, nemertina, isópoda, asteroidea, kinorhyncha, sipunculida and
275 acari.

Meiofaunal abundance was highly heterogeneous across the GoM and among cruises. Average abundance declined in successive cruises X-1 (282 ± 105 ind 10 cm^{-2}) followed by X-2 (219 ± 62 ind 10cm^{-2}) and X-3 (157 ± 50 ind 10 cm^{2}). Localized temporal variation was also evident; for instance, sampling 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, turbellaria and oligochaeta in X-1, and copepoda and turbellaria in X-2 and X-3, except that in X-3 turbellaria outnumbered copepoda, whereas the other major taxa were rare in all cruises.

Environmental variation and community correlates

Different environmental characteristics on each sampling station at each cruise were found, and that scenario is concordant with SS or MS paradigms. 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. 3a). 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. 3b). 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. 3c). PCA results suggest that sediment characteristics (%silt and %sand) and depth are the main environmental factors contributing to environmental heterogeneity among sampling stations.

Meiofaunal abundance correlated significantly with certain CAP scores, with the first in X-1 and with the second in X-3 (Fig. 4). In X-1, the relation was negative ($r = -0.77$; $p < 0.05$) and the CAP had negative loadings with inorganic carbon, oxygen and sand%, and positive loadings with depth and latitude (Fig. 4a). 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 negative and nearly significant ($r = 0.48$; $p = 0.066$) (Fig. 4b).

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 MS 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 region described as Marl[38], indicating that observed differences occur within and not among sedimentary regions.

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. Forty-nine percent of identified organisms were distributed among 9 genera: *Aphelencoides*, (12.9%), *Microlaimus* (7%), *Desmoscolex* (6%), *Halalaimus* (5.8%), *Molgolaimus* (3.9%), *Diplopeltula* and *Amphimonhy* (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 C22 was the least diverse station (H' = 3.8, S = 17) (Table 2).

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. 5a) 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 in those communities, followed by groups 2A, 1B and 2B (Fig. 5b). 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. 5c). 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 by larger fraction of colonizers (Fig. 5d).

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).

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 C22, 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. 6a) (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 ($r = 0.63$, $p < 0.01$, bootstrap c.l 0.33 – 0.94) indicating that differences in genus richness increases with geographic separation (Fig. 6b). The total compositional difference among nematode communities β_{cc} did not show a significant relationship with geographical distance (Fig. 6c), 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.

Environmental distance among sampling stations, including all environmental variables, were positively correlated with geographic distance (Fig. 7a) ($r = 0.87$, $p < 0.05$). This finding indicates that environmental differences increase with an increasing geographic distance among stations. On the other hand, we found a positive correlation between environmental distance and β_{cc} (Fig. 7b) ($r = 0.65$), $p < 0.05$). 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.

Given our results, we may suggest that meiobenthic communities from the GoM are influenced by the particular environmental characteristics of sediments and that dispersal does not play a pivotal role on community structure. Hence we propose that meiobenthic communities from GoM follow the SS model.

Discussion

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[33–36,38]. 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. 3). 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[5,29,49]. 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[50,51]. 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.

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[52]. Likewise, sediment size and type may be important in structuring meiobenthic communities and in determining seafloor heterogeneity[5]. 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 increased 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 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[53]. Hence, depth is correlated with a decrease in POC export from surface to the deep-sea and with decreased meiobenthic abundance[11].

Total community structure

Nematoda, copepoda and turbellaria were the most abundant groups in all sampling periods; whereas gastrotricha, tardigrada, polichaeta, loricifera, oligochaeta, among others, were rare, and has been described in other deep-sea sediments[52]. Nematodes have been recognized as the most abundant group in meiobenthic communities, almost always exceeding 75% of the total number of meiobenthic organisms. However, values as low as 50% have been found at depths exceeding 1000m in oligotrophic areas of the central Arctic Basin[45], in the tropical central part of the Indian Ocean[54,55], and in the tropical Atlantic[56], 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 region[38], suggesting that sediment type is not the main

443 factor influencing the community structure, but has a synergic effect with other environmental
444 drivers (Table 1).
445
446 Nematode community: Functional and maturity stage
447
448 Feeding strategies of nematofauna have been shown to vary with depth, mostly due to
449 morphological differences, as well as their abundance and diversity influenced by organic matter
450 input to the sediment[57]. We found that ITD and the proportion of functional groups of nematode
451 communities are similar among samples. Sampling stations with the highest ITD wereA1, B18
452 and C22, that means the proportion of four functional groups are more even compared with the
453 other sampling stations, a pattern bearing no association with depth. The fact that most nematodes
454 (>=50% in all sampling stations) belong to group 1A reflects the prevalence of bacterivory in deep-
455 sea communities. It has been suggested that greater ocean depths harbor smaller bacterial cells in
456 benthic environments of the GoM and that bacterial biomass decline significantly with depth[58]. In
457 contrast, no significant relationship has been found between bacterial abundance and biomass with
458 depth, according to a random forest model for the same region[3]. The preponderance of trophic
459 group 1A in nematode communities suggests that the trophic web supporting them is based on
460 bacterial production as the most important resource; on the other hand, the MI values between 2.6
461 and 3.1 of the same communities indicate that they are composed by an admixture of colonizer
462 and persister genera. Nevertheless, the MI of each trophic group revealed that groups 1A and 2B
463 are comprised of more persister and mature genera (Fig. 5d). On the other hand, groups 1B and
464 2A are characterized by colonizer organisms[14]. This suggests that ecological interactions among
465 organisms within the persisters group are more stable and that its high dominance may be due for
466 at least to two reasons. First, bacterial biomass is not a limited resource, and second, niche

diversification among nematodes, detectable at genus level, avoids competition. It has been suggested that a limited input of organic matter may enhance niche diversification and species dominance[59], in fact, the deep-sea sediments from GoM is dominated by at least three genera sharing the same feeding type.

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, a finding suggesting that functional structure may be independent of environment or ecological factors for deep-sea nematode communities.

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[25,61]. 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. 6c) and its partition in replacement and richness suggest that compositional differences among sites (β_{cc}) are the result of different processes

governing community structure in different regions of the Gulf (Fig. 6). In this way, mechanisms such as selective extinctions, colonization, dispersal limitation, among others, may influence replacement and taxon richness differences among communities[62–64].

Based on our results we may suggest a close relationship of environmental characteristics and nematode community structure (Fig. 7). 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[1]. 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[38], which is an admixture of pelagic carbonate sediment, foraminifers and coccoliths, and terrigenous clay. Thereby, the similarity of communities separated by less of 200 km (Fig. 6c) may be due to sampling stations sharing the same sediment type.

Conclusion

The variability in species composition results from the integration of ecological and evolutionary processes operating at different spatial and temporal scales. At local spatial scales (1-10m) species are controlled by processes involving resource partition, competition, predation, facilitation, physical disturbance, and recruitment. At a regional scale (100s to 1000sm) factors such as environmental gradients, dispersal, metapopulation dynamics and habitat heterogeneity are very important[65].

Here, we were able to use the metacommunity theory to study the meiobenthic and nematode communities of the GoM and in this way 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.

Author contributions

José Alejandro Cisterna-Céliz conceived the paper, identified meiobenthos from X3, carried out data analyses, interpreted results and wrote the paper.

Mirayana Marcelino-Barros identified meiobenthos from X1, X2 and X3 and nematode community from X1 and contributed to data analyses.

Axayácatl Rocha-Olivares supervised the research and contributed to interpretation of results and writing. All of the authors reviewed and approved the manuscript.

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699 **Figures**

700 Figure 1. Sampling stations within Gulf of Mexico. Figure created using Ocean Data View (version
701 4.5.6, Schlitzer, R., 2013. "https://odv.awi.de".

702 Figure 2. Regression analysis of meiofaunal abundance in the entire sample (total abundance)
703 against abundance estimated from 25% aliquots (aliquot abundance) in samples from X-2 and X-
704 3 cruises used to estimate total abundance in X-1 samples. Blue circles: X-2 and Orange circles:
705 X-3.

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

709 Figure 4. Meiofauna abundance (ln) correlated against environmental CAP. a) X-1, b) X-2 and c)
710 X-3. TOC: Total Organic Carbon; IC: Inorganic Carbon. Red rectangles mean positive loading
711 and blue rectangles mean negative loadings. Loading in X-2 are not included because the
712 correlation was not significant.

713 Figure 5. Index of Trophic Diversity (1-ITD) and Maturity index (MI) for nematode communities.
714 a) ITD at each sampling station, b) proportion of trophic groups at each station, c) MI at each
715 sampling station, d) MI at each functional group.

716 Figure 6. β diversity results correlated with geographic distance (Km). a) β_{-3} diversity, b) β_{rich}
717 diversity and c) β_{cc} diversity. In Figure a) blue circle include paired comparisons of sampling
718 stations E40, E3, E36, E35, E43 (group 1) and red circle include comparisons with sampling station
719 E15 and E27 (group 2).
720
721 Figure 7. Euclidean Distance (E.D.) of environmental variables from paired-comparisons of all
722 sampling stations from X-1. a) E.D. including all environmental variables, and b) E.D. of scores
723 from CAP analysis of X-1.
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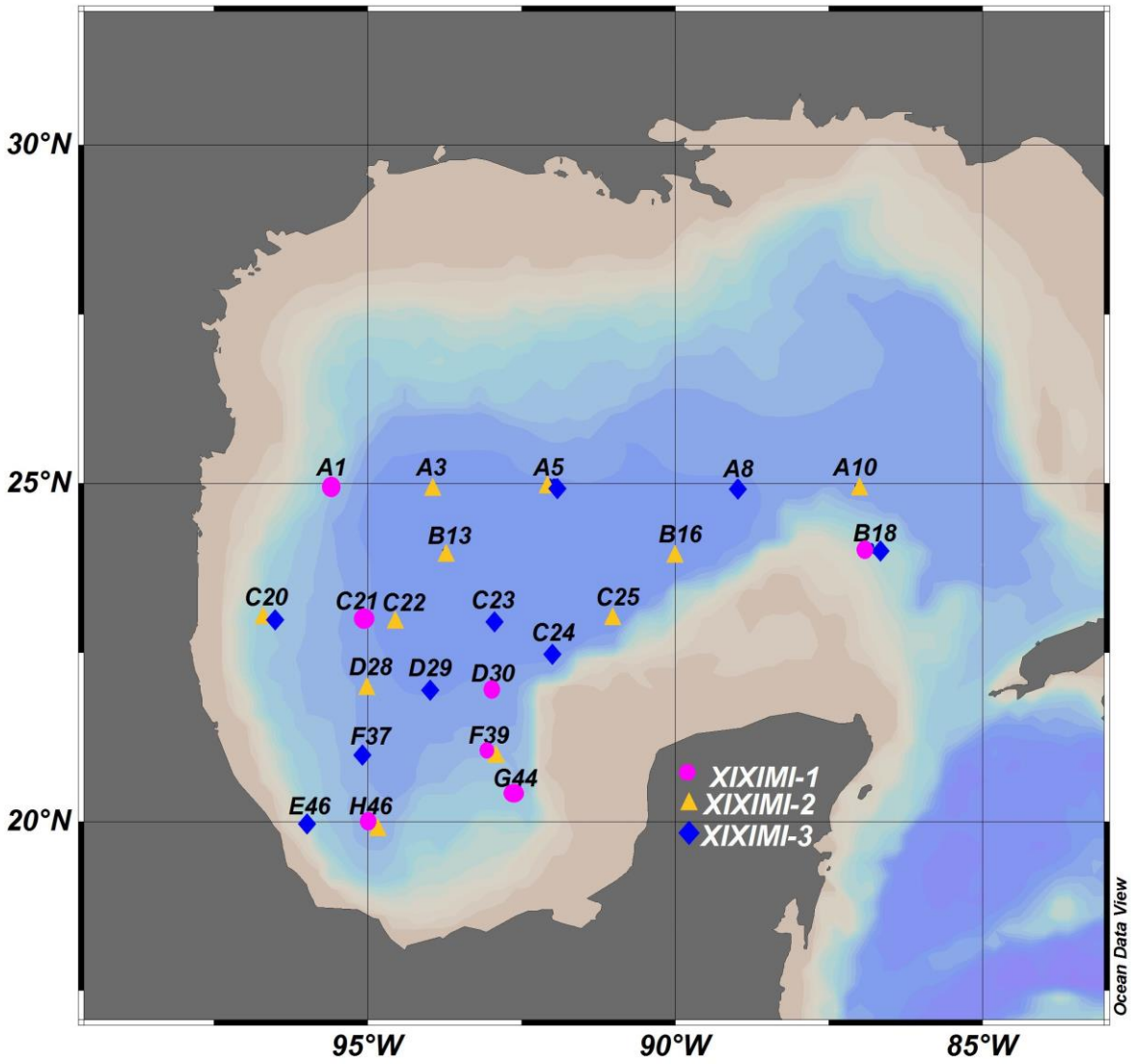

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730 Figure 1.

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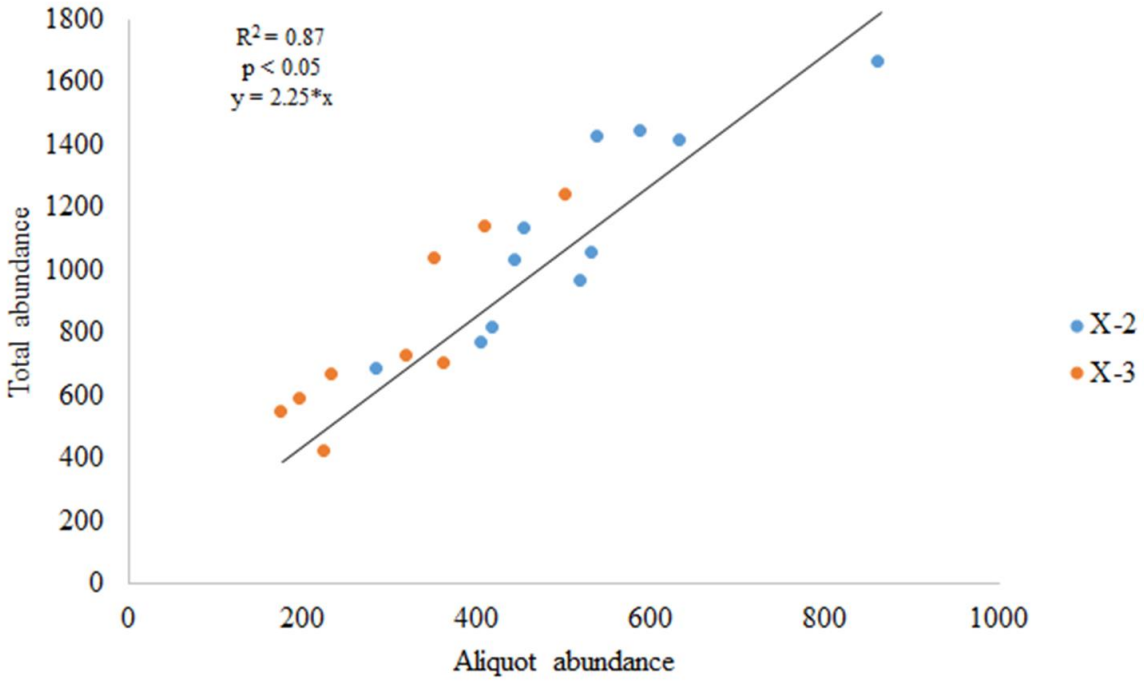

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734 Figure 2.

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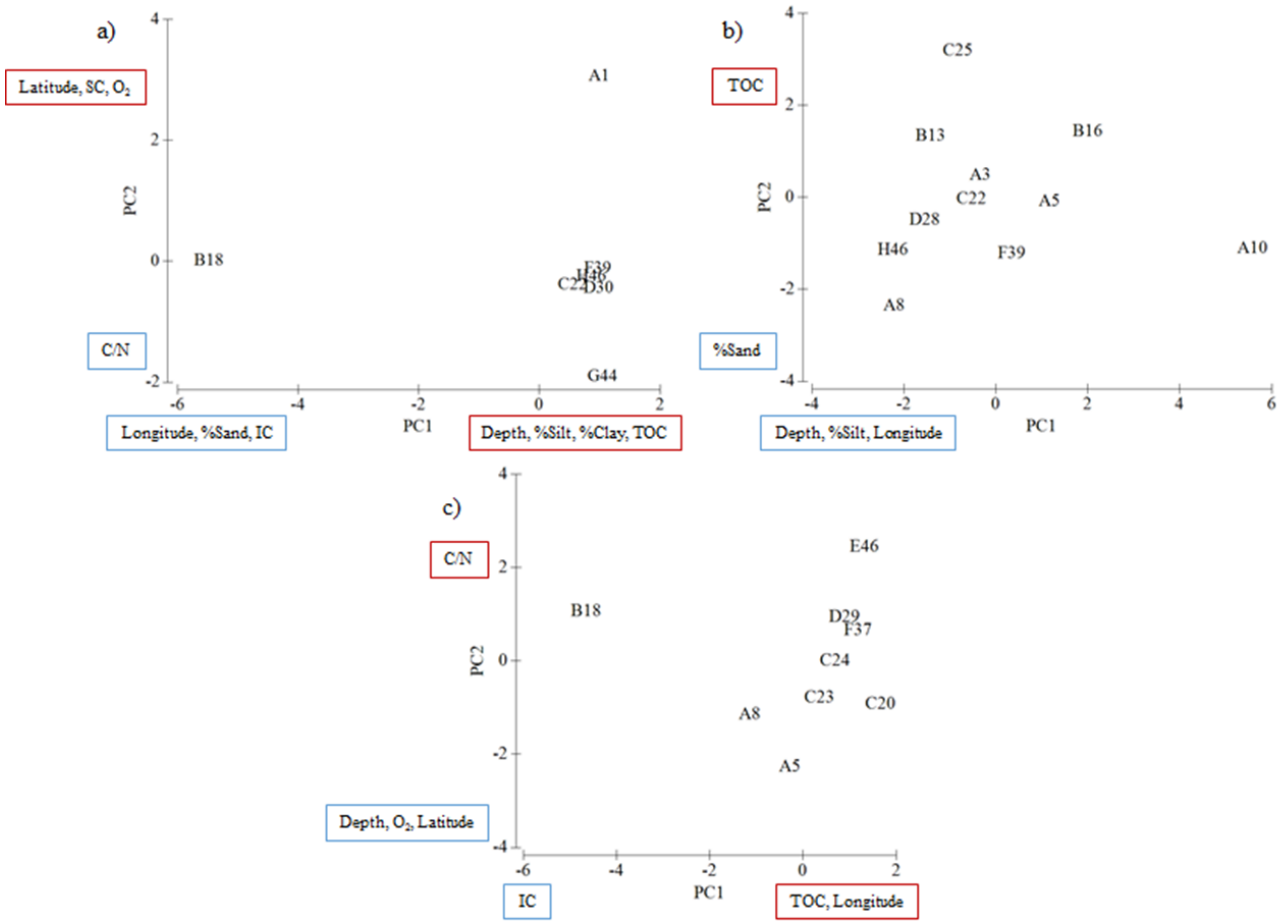

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738 Figure 3.

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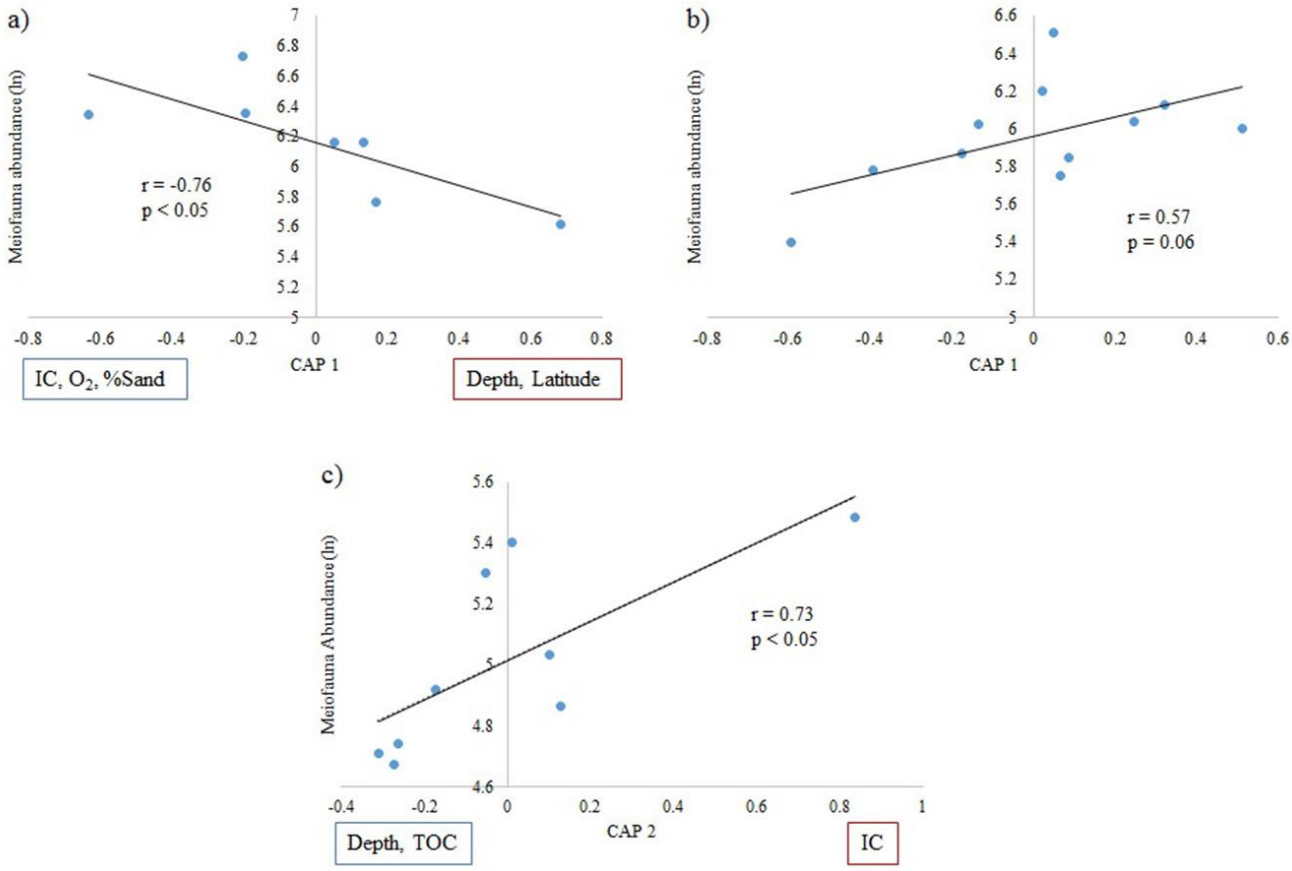

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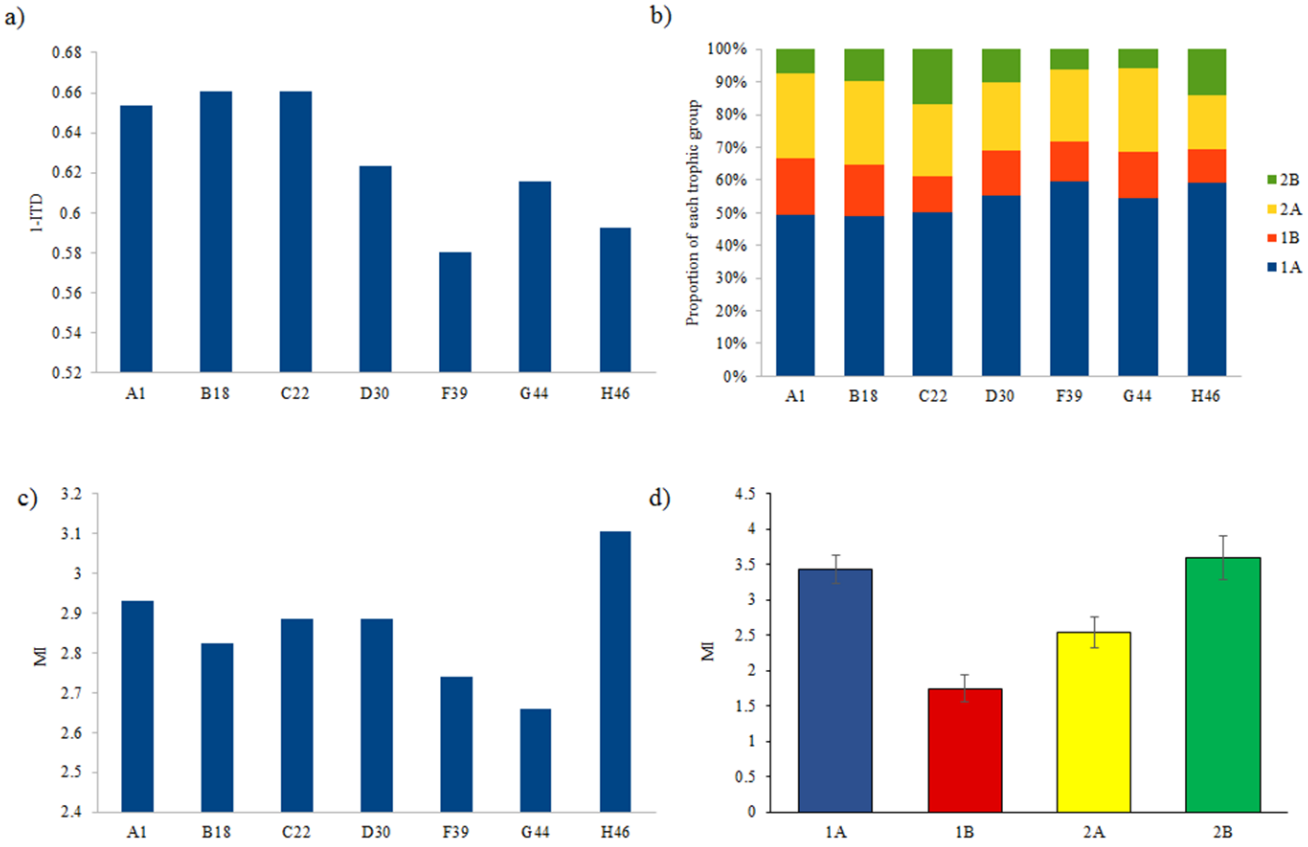

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747 Figure 5.

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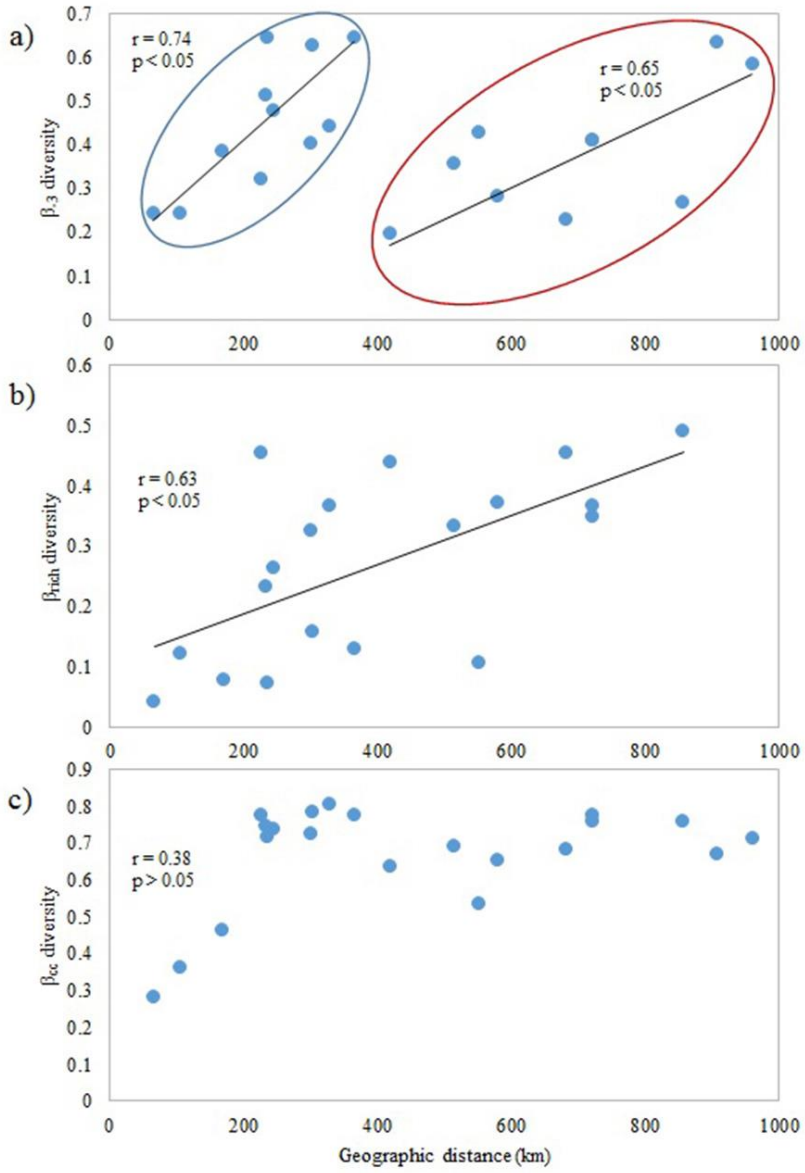

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752 Figure 6.

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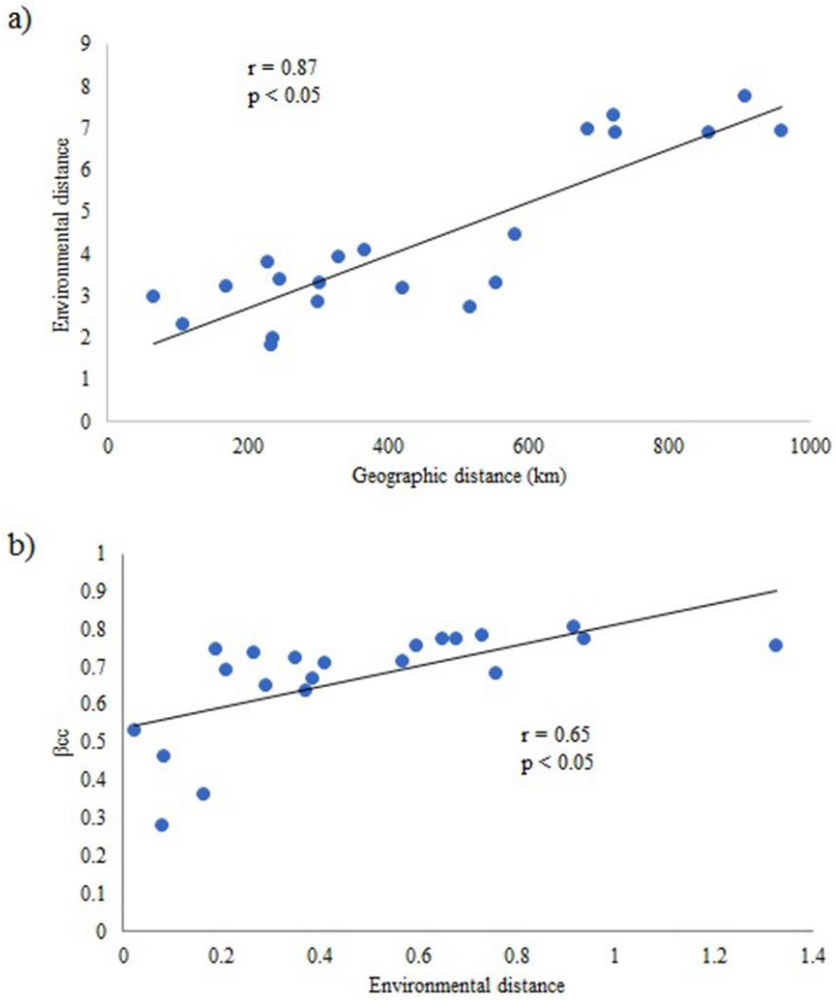
a)
r = 0.87
p < 0.05
Environmental distance
Geographic distance (km)
b)
r = 0.65
p < 0.05
βcc
Environmental distance

Figure 7.

Tables

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	1.890	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			

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

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