

Research Article

Assessment of Longitudinal Gradients in Nematode Communities in the Deep Northern Gulf of Mexico and Concordance with Benthic Taxa

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Meiobenthic nematode assemblages were examined at 16 stations along two transects on the eastern and western boundaries of the deep northern Gulf of Mexico (dNGOM) at depths of 212–3000 m. The highest abundance (297 individuals 10 cm⁻²) and number of genera (71) occurred at stations near the Mississippi River delta. Number of genera decreased with increasing depth, and showed differences in community composition between the east and west regions. The dominant family, Comesomatidae, was represented by *Sabatieria* that was present at most shallow stations but absent at greater water depths. A significant difference in nematode feeding morphology was observed between depth groups but not between the two transects at different longitudes. Patterns of nematode community structure are congruent with harpacticoid copepods. Overall, the higher abundance and diversity of nematodes in the north-central Gulf of Mexico is consistent with findings of other benthic taxa and reflects organic material loading from the Mississippi River driving deep sea communities in the Gulf. The east-west gradient in composition of nematode communities suggests that nematode assemblages have well-defined distribution patterns similar to other meiobenthic taxa in the GOM but they are not aligned in the bathymetric zones observed in macrofauna, megafauna and demersal fishes.

1. Introduction

Deep-sea biodiversity remains woefully understudied, and it is estimated that only 1% of marine species is currently described [3]. Most studies of deep-sea benthic diversity are based on mega- or macrofaunal organisms, but studies of the meiobenthos and nannobenthos have revealed a diverse fauna [4–6]. Meiobenthic abundance and diversity exceed that of macrofauna and megafauna, and the biomass of the meiofauna community dominates that of macro- and megafauna with increasing water depth [7]. Comparison of biomass and respiration rates also suggests that meiofauna have greater rates of carbon flow through food webs in deeper waters in the Gulf of Mexico than the larger macrofauna and megafauna [8, 9].

As the numerically dominant meiofaunal taxon in deep-sea sediments, nematodes play significant roles in marine biogeochemical cycles through bioturbation and related processes that enhance sediment oxygenation and solute transport, thereby increasing rates of demineralization [10–12]. However, despite their numerical dominance, high diversity, and functional significance [13, 14], studies of this ubiquitous phylum are rare. Studies of nematode biodiversity in the deep sea conducted in the Pacific and Atlantic Oceans [15–19] reveal both latitudinal [20] and depth-related gradients [21–23]. Additionally, Danovaro et al. [24] observed a longitudinal gradient in nematode biodiversity in the Mediterranean Sea that was related to surface primary production and sediment organic matter. It appears that the spatial biodiversity and distribution of

nematodes are affected by deep-sea habitat heterogeneity [6], further supporting the broader contention that habitat heterogeneity plays an important role in maintaining deep-sea species diversity [25] across taxa and size classes.

To date there is little information available on nematode distribution in the northern Gulf of Mexico, with most studies conducted in the intertidal zone. A recent checklist of the free-living marine nematodes of the Western North Atlantic and Gulf of Mexico [2] lists 190 species, all of which occur in shallow waters of the continental shelf. Of these 66% was endemic, and the identifications are also associated with poor taxonomic descriptions to confirm identifications [26]. Cobb [27], Chitwood [28], and Chitwood and Timm [29] described the free-living marine nematodes of various habitats from the Texas coast. Intertidal nematodes in the coastal northeastern Gulf of Mexico were studied by King [30], Hopper [31], and Keppner [32]. The first studies of subtidal nematodes in this region were conducted in the East Flower Garden Banks [33–36] at a brine seep at 70 m water depth. The nematode fauna of the Caribbean has been described by Boucher and Gourbault [37], de Jesus-Navarrete and Herrera-Gomez [38], and de Jesus-Navarrete [39]. Castillo-Fernandez and Lamshead [40] have also described nematodes from the southern GOM. However, nematode collections from the deep GOM have been limited to ecological studies of the meiofaunal community as a whole [41]. Due to the significant economic importance of the GOM and the inevitability of future oil and gas exploration in deep water, it is critical to understand the regional differences of its biodiversity.

Here we present the first ecological study of nematode assemblages in the deep northern GOM, specifically investigating patterns of nematode community structure over depth and longitude in the northern deep GOM. The north-central and northeastern GOM are characterized by strong river outflow of nutrients and organic matter that serve to enhance surface primary production and fuel-enhanced benthic secondary production. Surface productivity patterns have been well characterized [42], and physical oceanographic conditions create a favorable environment for primary productivity in an otherwise oligotrophic subtropical basin [43]. Specifically, in the northeastern region the Loop Current, Loop Current Eddies, and other smaller cyclonic and anticyclonic eddies transport nutrient-rich shelf waters onto the continental slope [43]. Comparatively, the northwestern GOM receives relatively less river outflow and is relatively more oligotrophic [42].

The analysis of Baguley et al. [41] revealed a strong influence of organic matter outflow from the Mississippi and Atchafalaya Rivers in northeast GOM on meiofauna communities. Additionally, Baguley et al. [41] reported a significant longitude by depth interaction of the meiofauna community abundance in the northern GOM and associated interactions with seafloor topographic features such as the Mississippi Trough, DeSoto Canyon, and Florida Escarpment. The distribution patterns of several macrofaunal taxa in the GOM are associated with surface phytoplankton production and show a horizontal distribution pattern that is related to the organic input of the Mississippi River [44].

Therefore, nematode assemblages may differ by longitude in the northern GOM in response to longitudinal variations in physical, chemical, and biological water column processes [42–44]. To test this hypothesis, we examined (1) the composition of the nematode community along depth and longitudinal gradients, (2) the structure of the nematode community in relation to water depth and longitude gradients, (3) the functional diversity of the nematode community as determined from the morphology of the buccal cavity, and (4) compared the community structure patterns of nematode spatial variability with that of Harpacticoida and Polychaeta. This study also provides a valuable baseline dataset for comparison with potential future environmental perturbations such as the Deepwater Horizon oil spill from April 20–July 15, 2010.

2. Materials and Methods

2.1. Field and Laboratory Methods. Nematode biodiversity and community structure were analyzed at 16 stations in the northern GOM deep sea (Figure 1). Thirteen of 16 stations were along two transects in the northeastern (S39–S44) and northwestern (RW1–RW6, AC1, Alaminos Canyon) GOM that spanned a depth range of 212–3000 m. All stations were sampled as part of the Deep Gulf of Mexico Benthos (DGoMB) program during summer, 2000 [45]. Detailed field and laboratory sampling and sorting procedures are outlined by Baguley et al. [5, 41]. Briefly, samples were collected with a 0.2 m² GOMEX boxcorer equipped with an array of smaller subsampling corers attached by hose clamps along a central stainless steel bar within the box. Meiofauna subcores had a 5.5 cm inner diameter and penetrated approximately 15 to 30 cm into the sediments. The top 3 cm of sediment was retained for examination, as it has been shown to contain over 80% of the meiofauna in deep-sea GOM samples [5]. Five replicate core samples were obtained from each of the sixteen stations. The taxonomic study of nematodes was initiated about 4 years after samples were collected and thus replicates from some stations were lost due to desiccation prior to taxonomic analysis. Only three replicates were analyzed from C1 and AC1. Only four replicates were analyzed from stations RW5, RW6, and S44.

In the field, meiofauna were narcotized with 7% MgCl₂ and preserved in 5% buffered formalin. In the laboratory, fine sediments were removed by rinsing samples through a 45 μm mesh sieve. Meiofauna retained on the 45 μm mesh sieve were extracted from coarser sediments and other debris using the Ludox centrifugation method of de Jonge and Bouwman [46]. Nematodes were hand picked under a Wild M3 stereoscope and transferred to ethanol and then cleared in glycerol by the method of Seinhorst [47] for identification on a Zeiss Axioskop.

2.2. Nematode Taxonomy. Standard identification keys and manuals [48] were used for taxonomic identification to genus level based on morphological characteristics. Data on nematode distributions at the species level are scarce and most deep-sea nematodes are undescribed, and thus it has

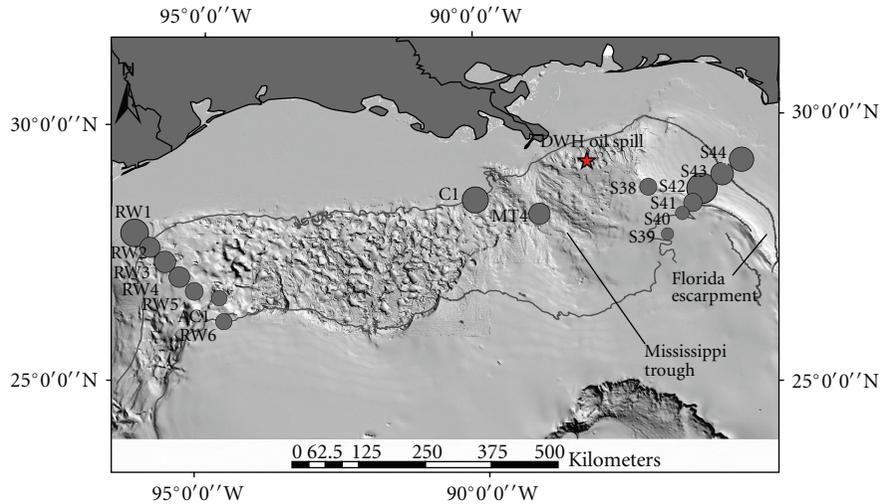


FIGURE 1: Spatial analysis of nematode abundance ($N\ 10\ cm^{-3}$) at dNGOM stations. Bubble size equals relative nematode abundance.

been practical to identify nematode morphotypes to genus [49]. Many characters to distinguish species are based only on males and furthermore juveniles are indistinguishable beyond the genus level. Vanreusel et al. [6] note that several studies indicate that genus composition is an indicator of macroecological patterns. The samples will be archived at the National Museum of Natural History, Washington, DC, USA.

2.3. Feeding Groups. Genera were classified into four feeding groups based on buccal morphology, namely, 1A (selective deposit feeders), 1B (nonselective deposit feeders), 2A (epi-growth feeders), and 2B (omnivores and predators) [50]. Although Moens and Vincx [51] have proposed a broader classification into six feeding groups, the original categories proposed by Wieser [50] are used here because several genera from this region have not yet been described, and thus little information is available for them.

2.4. Statistical Analysis. Genus richness and evenness of nematodes were regressed against depth to determine the effect of this variable. Multivariate analyses were performed using PRIMER 6.1 [52]. Ordination of samples was performed using nonparametric multidimensional scaling (nMDS) to visualize the similarity patterns [53]. Jaccard similarity index was used to calculate similarity among samples after transformation for presence/absence of genera due to unequal sample size as a result of loss of some replicates and the ability of this transformation to downweigh the effect of common species [53]. Multivariate statistical differences in community structure over depth and longitude were determined using two-way crossed Analysis of Similarities (ANOSIM) where global $R = 1$ indicates complete separation of groups and global $R = 0$ indicates no separation [53]. Diversity analysis was also calculated using PRIMER 6.1 to determine the evenness of genera in each sample (Primer-E Ltd.). SIMPER analysis was used to investigate longitudinal differences in genus and family abundance and

percent contribution to community structure. Similarity profile (SIMPROF) tests were performed on group average cluster analyses to test the null hypothesis that longitudinal differences in nematode community structure do not exist in the northern Gulf of Mexico deep sea.

2.5. Cross-Taxon Spatial Variability. The community structure patterns of nematode spatial variability were compared with that of Harpacticoida and Polychaeta using the RELATE procedure in Primer, which tests for matching among the station patterns computed using the Bray-Curtis similarity resemblance matrices. This is testing to determine if MDS patterns for the three groups are the same. This comparison can only be made where genus or species level identifications were performed and the organisms were found. This occurred only at the following 13 stations: AC1, C1, RW1, RW2, RW3, RW4, RW5, RW6, S35, S38, S39, S40, and S43.

3. Results

3.1. Abundance. At the 16 stations investigated here for nematode community structure, abundance ranged from roughly $53\text{--}300$ individuals $10\ cm^{-2}$ (Table 1). Nematode abundance decreased with depth along both transects (Figure 2). The highest abundance, 267 individuals $10\ cm^{-2}$, occurred at station C1 (depth 482 m) near the mouth of the Mississippi delta. The lowest abundance, 53 individuals $10\ cm^{-2}$ occurred at station S39 in the eastern transect.

3.2. Taxonomic Composition and Diversity. A total of 4764 nematode individuals were identified (Table 2) from the 16 stations, representing 128 nematode genera and 35 families. The highest number of genera (71) occurred at station S43 (depth 362 m) in the eastern transect and the lowest number of genera (23) occurred at station RW6 (depth 3000 m) in the western transect. The cumulative percent composition of 42 genera in the total nematode fauna examined is less than

TABLE 1: DGoMB station locations, depth, and average meiofaunal abundance (average of five replicate cores) for pooled taxonomic groups.

Station	Latitude	Longitude	Depth	Abundance (N/10cm ²)
RW1	27.50014	-96.0029	212	277 ± 50
RW2	27.25403	-95.7468	950	145 ± 80
RW3	27.00836	-95.4924	1340	173 ± 16
RW4	26.75142	-95.2502	1575	164 ± 30
RW5	26.50753	-94.9967	1620	116 ± 50
AC1	26.39357	-94.5731	2440	92 ± 33
RW6	25.99730	-94.4956	3000	100 ± 40
S44	28.74999	-85.7477	212	221 ± 43
C1	28.05984	-90.2499	336	267 ± 134
S43	28.50294	-86.0768	362	209 ± 51
S42	28.25100	-86.4193	763	134 ± 33
MT4	27.82761	-89.1662	1401	172 ± 29
S38	28.27995	-87.3276	2627	97 ± 27
S40	27.83948	-86.7514	2972	60 ± 11
S41	28.01364	-86.5734	2974	65 ± 17
S39	27.48368	-86.9998	3000	53 ± 15

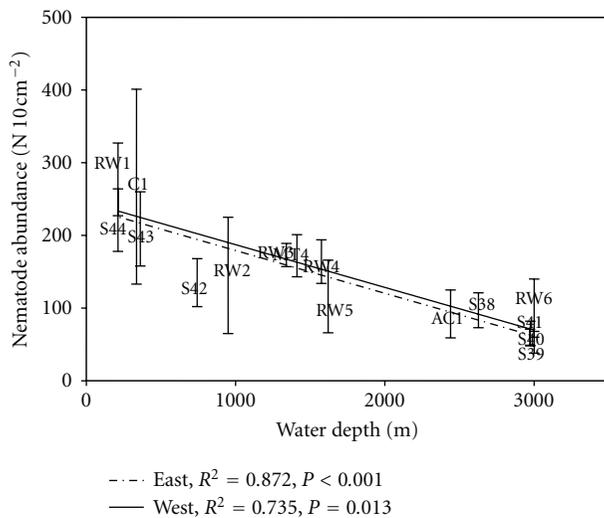


FIGURE 2: Abundance of nematodes as a function of depth at eastern and western transects in dNGOM.

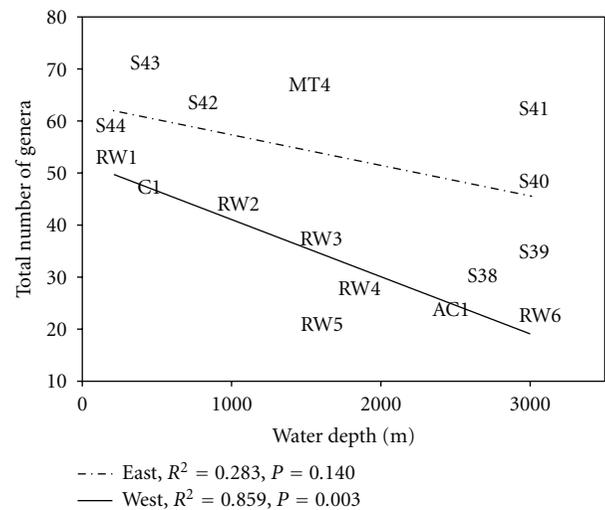


FIGURE 3: Number of nematode genera as a function of depth in eastern and western transect in dNGOM.

0.1%, and 103 genera comprised less than 1% of the total fauna indicating the presence of many rare genera (Table 2). Our study is the first record of 56 genera that have not been recorded previously in the GOM [2].

The average number of genera decreased with increasing water depth in both transects, but the correlation to water depth was stronger in the western transect (Figure 3). The average number of genera in the eastern transect was higher than in the western transect. The evenness of genera increased with water depth in both transects from 0.69 at 362 m to 0.94 at 2440 m depth (Figure 4).

A two-way crossed analysis of similarities of genera abundance indicated significant depth differences between

all longitude groups ($P = 0.001$; global $R = 0.925$) but no significant difference between all depth groups (Table 3). A hierarchical cluster analysis based on Jaccard similarity coefficient of nematode genera shows a high level of similarity among the stations grouped by transects over depth that are located at different longitudes (Figure 5). The nMDS ordination of genera shows a clear separation of the east and west transects with stations RW6 and S38 most dissimilar (Figure 6). A separation of the nematode fauna in east and west transects is also noted by the high R values in the ANOSIM analysis of both the genera and family composition (Table 3).

TABLE 2: Nematode taxa in meiofaunal samples in the dGOM (listed by systematic scheme of de Ley and Blaxter [1]). Table includes order (in capital letters), family, genus, trophic guild assignment, and cumulative percent contribution of a genus to total nematode fauna. Genera not recorded previously in the GOM [2] are marked*.

Family/genus	Guild	Total abundance (cumulative % contribution)
ENOPLIA		
Benthimermithidae		
<i>Benthimermis</i> *	1A	3 (0.06)
Rhaphotothyreidae		
<i>Rhaphotothyreus typicus</i> *	1A	2 (0.04)
Thoracostomopsidae		
<i>Enoplolaimus</i>	2B	27 (0.57)
<i>Enoploides</i>	2B	8 (0.17)
<i>Mesacanthion</i>	2B	4 (0.08)
<i>Paramesacanthion</i> *	2B	1 (0.02)
<i>Thoracostomopsis</i> *	2B	1 (0.02)
Anoplostomatidae		
<i>Anoplostoma</i>	1B	2 (0.04)
<i>Chaetonema</i> *	1B	1 (0.02)
Phanodermatidae		
<i>Crenopharynx</i>	1A	1 (0.02)
<i>Phanoderma</i> *	1A	67 (1.41)
<i>Phanodermopsis</i>	1A	6 (0.13)
Anticomidae		
<i>Anticoma</i>	1A	8 (0.02)
Ironidae		
<i>Dolicholaimus</i>	2B	2 (0.04)
<i>Syringolaimus</i>	2B	49 (1.03)
Oxystominidae		
<i>Halalaimus</i>	1A	276 (5.79)
<i>Litinium</i> *	1A	4 (0.08)
<i>Nemanema</i> *	1A	4 (0.08)
<i>Oxystomina</i> *	1A	17 (3.59)
<i>Thalassoalaimus</i> *	1A	49 (1.03)
<i>Wieseria</i> *	1A	3 (0.06)
Oncholaimidae		
<i>Oncholaimus</i>	2B	8 (0.17)
<i>Viscosia</i>	2B	17 (0.36)
Enchelidiidae		
<i>Eurystomina</i>	2B	21 (0.44)
<i>Bathyeurystomina</i> *	2B	14 (0.29)
<i>Pareurystomina</i>	2B	9 (0.19)
<i>Calyptonema</i>	2B	19 (0.40)
<i>Symplocostoma</i>	2B	7 (0.15)
Rhabdodemaniidae		
<i>Rhabdodemia</i> *	2B	8 (0.17)
Pandolaimidae		
<i>Pandolaimus</i> *	2B	1 (0.02)
Trefusiidae		
<i>Rhabdocoma</i> *	2B	7 (0.15)

TABLE 2: Continued.

Family/genus	Guild	Total abundance (cumulative % contribution)
Xenellidae		
<i>Xenella</i>	1A	3 (0.06)
CHROMADORIDA		
Desmoscolecidae		
<i>Calligyryus</i>	1A	28 (0.59)
<i>Greefiella</i>	1A	47 (0.99)
<i>Desmoscolex</i>	1A	121 (2.54)
<i>Desmoscolex 2</i>	1A	6 (0.13)
<i>Pareudesmoscolex*</i>	1A	5 (0.10)
<i>Quadricoma</i>	1A	6 (0.13)
<i>Tricoma</i>	1A	(10.02)
Epsilonematidae		
<i>Epsilonema*</i>	1A	11 (0.23)
Draconematodae		
<i>Apenodraconema*</i>	2A	5 (0.10)
Chromadoridae		
<i>Acantholaimus</i>	2A	1 (0.02)
<i>Actinonema</i>	2A	12 (0.25)
<i>Chromadora</i>	2A	45 (0.94)
<i>Chromadorina</i>	2A	15 (0.31)
<i>Dichromadora*</i>	2A	3 (0.06)
<i>Euchromdora</i>	2A	1 (0.02)
<i>Hypodontolaimus</i>	2A	5 (0.10)
<i>Neochromadora</i>	2A	8 (0.17)
<i>Neotonchus*</i>	2A	8 (0.17)
<i>Prochromadorella</i>	2A	76 (0.02)
<i>Ptycholaimellus</i>	2A	1 (1.59)
<i>Rhyps</i>	2A	1 (0.02)
Ethmolaimidae		
<i>Filitonchus*</i>	1A	1 (0.02)
Selachinematidae		
<i>Halichoanolaimus</i>	2B	68 (1.43)
<i>Richtersia*</i>	2A	4 (0.08)
<i>Selachinema*</i>	2A	38 (0.80)
<i>Synonchiella*</i>	2B	3 (0.06)
Cyatholaimidae		
<i>Pomponema</i>	2A	34 (0.71)
<i>Paracanthonchus</i>	2A	4 (0.08)
<i>Cyatholaimus*</i>	2A	79 (1.66)
<i>Longicyatholaimus</i>	2A	12 (0.25)
<i>Marylynnia</i>	2A	3 (0.06)
Desmodoridae		
<i>Acanthopharyngoides</i>	2B	1 (0.02)
<i>Desmodora</i>	2A	73 (1.53)
<i>Paradesmodora</i>	2A	1 (0.02)
<i>Spirinia</i>	2A	66 (1.39)
<i>Perspiria</i>	2A	1 (0.02)

TABLE 2: Continued.

Family/genus	Guild	Total abundance (cumulative % contribution)
Microlaimidae		
<i>Bolbolaimus</i>	2A	6 (0.13)
<i>Microlaimus</i>	2A	187 (3.92)
<i>Molgolaimus</i> *	2A	6 (0.13)
<i>Paramicrolaimus</i>	2A	1 (0.02)
Monoposthiidae		
<i>Monoposthia</i>	2A	1 (0.02)
Ceramonematidae		
<i>Ceramonema</i> *	1A	90 (1.89)
<i>Pselionema</i>	1A	1 (0.02)
<i>Pterygonema</i> *	1A	1 (0.02)
MONHYSTERIDA		
Xyalidae		
<i>Ammotheristus</i> *	1B	97 (2.06)
<i>Amphimonhystera</i> *	1B	161 (3.38)
<i>Cobbia</i> *	2A	7 (0.15)
<i>Daptonema</i>	1B	126 (2.64)
<i>Diplolaimella</i>	1B	14 (0.29)
<i>Elzalia</i>	1B	83 (1.74)
<i>Elzalia 2</i>	1B	6 (0.13)
<i>Gnomoxyala</i> *	1B	8 (0.17)
<i>Linhystera</i> *	1B	21 (0.44)
<i>Monhystera</i>	1B	227 (4.76)
<i>Paramonhystera</i>	1B	21 (0.44)
<i>Prorhynchonema</i> *	1B	11 (0.23)
<i>Retrotheristus</i> *	1B	7 (0.15)
<i>Rhynchonema</i>	1B	17 (0.36)
<i>Steineria</i> *	1B	2 (0.04)
<i>Stylotheristus</i> *	1B	1 (0.02)
<i>Theristus</i>	1B	73 (1.53)
<i>Xyala</i>	1B	3 (0.06)
Scaptrellidae		
<i>Scaptrella</i>	2B	77 (1.62)
Sphaerolaimidae		
<i>Sphaerolaimus</i> *	2B	144 (3.02)
<i>Metasphaerolaimus</i> *	2B	63 (1.32)
Siphonolaimidae		
<i>Siphonolaimus</i> *	2B	13 (0.27)
Linhomoeidae		
<i>Didelta</i>	1B	25 (0.52)
<i>Disconema</i> *	1A	3 (0.06)
<i>Terschellingia</i>	1A	16 (0.34)
<i>Desmolaimus</i>	1B	1 (0.02)
<i>Eumorpholaimus</i> *	1B	6 (0.13)
<i>Linhomoeus</i>	1B	80 (1.68)
<i>Paralinhomoeus</i> *	1B	5 (0.10)

TABLE 2: Continued.

Family/genus	Guild	Total abundance (cumulative % contribution)
AREOLAIMIDA		
Axonolaimidae		
<i>Axonolaimus</i>	1B	13 (0.27)
<i>Odontophora</i>	1B	3 (0.06)
<i>Pseudolella</i> *	1B	4 (0.08)
Comesomatidae		
<i>Cervonema</i> *	1B	153 (3.21)
<i>Comesoma</i> *	1B	7 (0.15)
<i>Sabatieria</i>	1B	1072 (22.5)
<i>S. hilarula</i>	1B	16 (0.34)
<i>Setosabatieria</i> *	1B	1 (0.02)
<i>Paracomesoma</i> *	1B	11 (0.23)
<i>Mesonchium</i>	1B	1 (0.02)
<i>Metacomesoma</i>	1B	1 (0.02)
<i>Dorylaimopsis</i> *	2A	14 (0.29)
Diplopeltidae		
<i>Araeolaimus</i>	1A	49 (1.03)
<i>Campylaimus</i> *	1B	15 (0.31)
<i>Diplopeltis</i> *	1A	28 (0.59)
<i>Southerniella</i> *	1A	2 (0.04)
Leptolaimidae		
<i>Alaimella</i>	1A	8 (0.17)
<i>Camacolaimus</i>	1A	3 (0.06)
<i>Leptolaimus</i>	1A	115 (2.41)
Plectide		
<i>Setoplectus</i> *	1A	8 (0.17)
Aegialoalaimidae		
<i>Aegialoalaimus</i> *	1A	11 (0.23)
<i>Cyartonema</i> *	1A	11 (0.23)
<i>Diplopeltoides</i> *	1A	17 (0.36)
Total Nematodes		4764

A SIMPER analysis showed 69% dissimilarity between the genera of the eastern and western transects. *Sabatieria* was the most abundant genus in both transects though it was almost absent at the deeper stations (Table 4). The average similarity among genera of the eastern transect was 45%, while at the western transect it was 38%. The average abundance of most genera was higher in the eastern transect. *Oxystomina* was the only genus that had a higher abundance in the western transect.

Two families, Comesomatidae and Xyalidae, accounted for 43% of the total nematode fauna (Figures 7(a) and 7(b)). The Comesomatidae and Xyalidae were dominant in both transects. Among the most abundant families, only the Oxystominidae had a higher percent composition in the western transect. A SIMPER analysis showed a 45% average similarity among the families of the western transect

and 44% average similarity among families of the eastern transect. Average dissimilarity between the families of the two transects was 59%.

3.3. Functional Diversity. A regression of nematode feeding group abundance versus water depths illustrates that they were distributed fairly evenly across all depths (Figure 8). The shelf and inner slope stations were characterized by high numbers of nonselective deposit feeders such as *Sabatieria*. Deeper stations had higher numbers of selective deposit feeders such as *Oxystomina* and *Halalaimus*. The feeding groups showed a high similarity within the eastern and western transects. The greatest dissimilarity between the two transects was in the higher occurrence of the epigrowth feeders in the eastern transect (Table 5). The epigrowth feeders were less abundant at the slope stations.

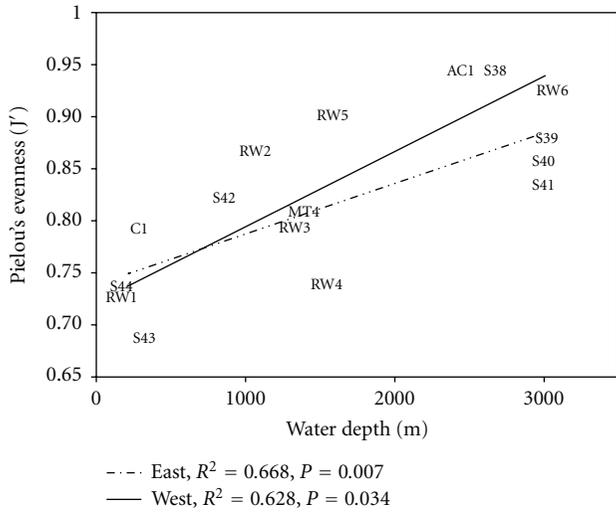


FIGURE 4: Evenness of nematode genera as a function of depth in eastern and western transects in dNGOM.

TABLE 3: R statistic values for ANOSIM test of the Bray-Curtis similarity matrices for pairwise comparison of longitudinal and depth differences in distribution of genera and family levels.

Pair-wise comparison	Global R	P value
Genus		
Longitude	0.925	0.001
Depth	0.326	ns
Family		
Longitude	0.650	0.003
Depth	0.338	ns
Feeding groups		
Longitude	0.269	ns
Depth	0.414	0.009

3.4. *Cross-Taxon Spatial Variability.* The Harpacticoida and Nematoda patterns match best (Rho = 0.249), but it is barely nonsignificant at $P = 0.057$. The patterns of the Polychaetes did not match the patterns for either nematodes or harpacticoids ($P > 0.1$) (Table 6).

4. Discussion

The GOM has significant economic importance and it is critical to understand the regional differences of its biodiversity. Our study confirms that nematodes are an abundant and diverse component of meiobenthos in the dNGOM and provides baseline data for a previously unexamined taxonomic group in this region. The proximity of eastern transect stations S38 and S40 to the Deepwater Horizon oil spill in April-July, 2011 reinforces the importance of this data for future environmental assessments.

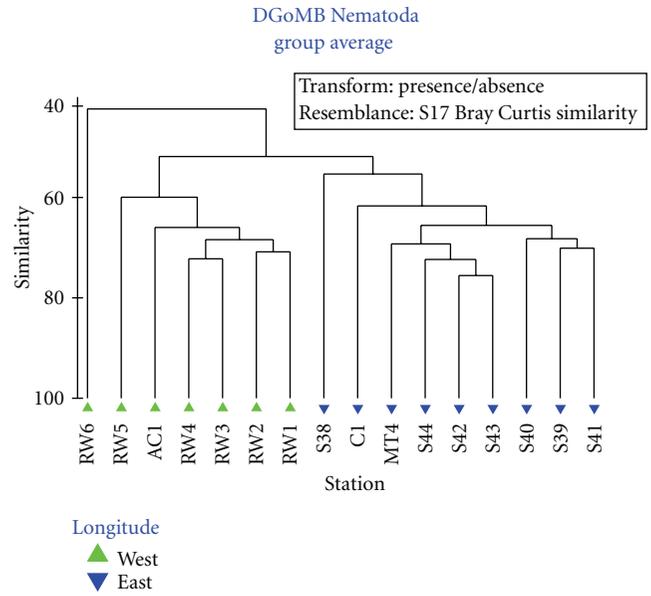


FIGURE 5: Hierarchical Cluster analysis with SIMPROF test on similarity of nematode genera at dNGOM stations and flower gardens brine seep.

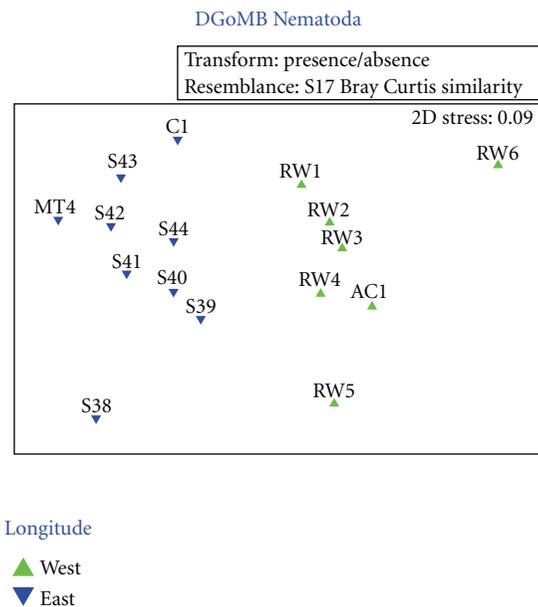


FIGURE 6: nMDS ordination of nematode genera abundance in dNGOM based on Bray-Curtis similarity of presence/absence data.

4.1. *Abundance.* A significantly higher abundance of nematodes and all meiofauna groups on the eastern transect was noted by Baguley et al. [41] to be associated with high chlorophyll-*a* biomass in the overlying water column. The lack of a significant overall difference in abundance in our study may be attributed to the small subset of stations investigated here. The decrease in nematode abundance with increasing depth seen in the northern Gulf of Mexico reflects trends similar to those observed in previous studies [54, 55].

TABLE 4: SIMPER (Similarity Percentages) analysis of 20 most common nematode genera at GOM eastern and western transects.

Genera	Groups West and East		Average dissimilarity = 68.83 Contribution%
	Group West Av.Abund	Group East Av.Abund	
<i>Sabatieria</i>	48	81.78	19.56
<i>Monhystera</i>	0.29	25	7.23
<i>Halalaimus</i>	12.57	20.89	4.2
<i>Oxystomina</i>	14.86	7.44	3.28
<i>Microlaimus</i>	7.57	14.89	3.2
<i>Cervonema</i>	7.43	11.22	2.65
<i>Sphaerolaimus</i>	3.57	13.22	2.63
<i>Spirinia</i>	0	7.33	2.41
<i>Amphimonhystera</i>	9.43	10.56	2.38
<i>Leptolaimus</i>	7	7.33	2.29
<i>Prochromadorella</i>	0	8.44	2.16
<i>Cyatholaimus</i>	0	8.78	2.14
<i>Daptonema</i>	5.14	10	2.12
<i>Scaptrella</i>	1.14	7.67	2.04
<i>Linhomoeus</i>	3	6.56	2.01
<i>Desmoscolex</i>	5	9.56	1.79
<i>Ceramonema</i>	3.57	7.22	1.67
<i>Theristus</i>	1.57	6.89	1.64
<i>Metasphaerolaimus</i>	6.71	1.78	1.63
<i>Elzalia</i>	4.86	5.44	1.59

A comparative study of meiofauna from shelf and deep-sea sites off the S.E. coast of Brazil by Netto et al. [56] described the relative abundance of nematodes in the meiofauna that increased with depth. Vincx et al. [57] also note that exceptions to decreased density of meiofauna with increasing depth may be attributed to local physiographic variations. Such variation was also observed in our study where station S42 above the Florida Escarpment had a higher nematode abundance than other shallower stations. Baguley et al. [41] attributed a midbathyal meiofauna abundance maximum in the deep northeast GOM to interactions between seafloor topography, Mississippi River outflow, and the Loop Current. The overall decrease in nematode abundance with increasing water depth is related to the decreasing supply of organic matter away from land [4, 8, 58]. Morse and Beazley [59] also found a strong correlation between organic matter content and macrofauna biomass in the northern GOM. Exceptions to decreasing abundance and biomass with increasing water depth in the Mediterranean are associated with trophic gradients [60]. Though such trophic gradients are not defined in the GOM, the distribution of benthic organisms is related to surface phytoplankton production and associated particulate organic carbon flux to the benthos [44].

4.2. Diversity of Nematode Assemblages. The nematode fauna identified here represents a deep sea assemblage that is distinct from the intertidal and shallow subtidal studies of the GOM [32, 36]. The lack of significant differences in the

composition of the nematode community between different deep sea sampling depths was also noted by Danovaro et al. [19]. They attributed the lower biodiversity at canyons to unique hydrodynamic conditions that were also noted by Baguley et al. [5]. The two stations that are less than 40% similar to their respective transects were RW6, located in the West lower slope and S38, located in the East Lower slope faunal zone classification of Wei et al. [44]. The nematode community at Alaminos canyon (station AC1) was closer to that of other stations in the western transect than that of RW6. The low similarity of the community at RW6 to other stations of this transect may be due to its depth at 3000 m. The Chromadoridae, Desmodoridae, and the genus *Sabatieria*, that were dominant at the slope stations, were absent at this station. The low similarity of the nematode community at station S38 to the other stations of this transect may be due to its separation from the Florida escarpment where impingement of the Loop current results in upwelling of nutrients [61]. Large scale comparisons of nematode community structure in other ocean basins indicate that continental shelf nematode communities were significantly different from slope communities, while there was no significant difference between slope and abyssal plain communities [6]. The lack of a significant difference between the genera and family depth groups suggests a more even distribution of nematode taxa at greater water depths (Table 3). This pattern supports the observations of harpacticoid diversity in the deep GOM, where there are proportionally more higher order taxa and therefore

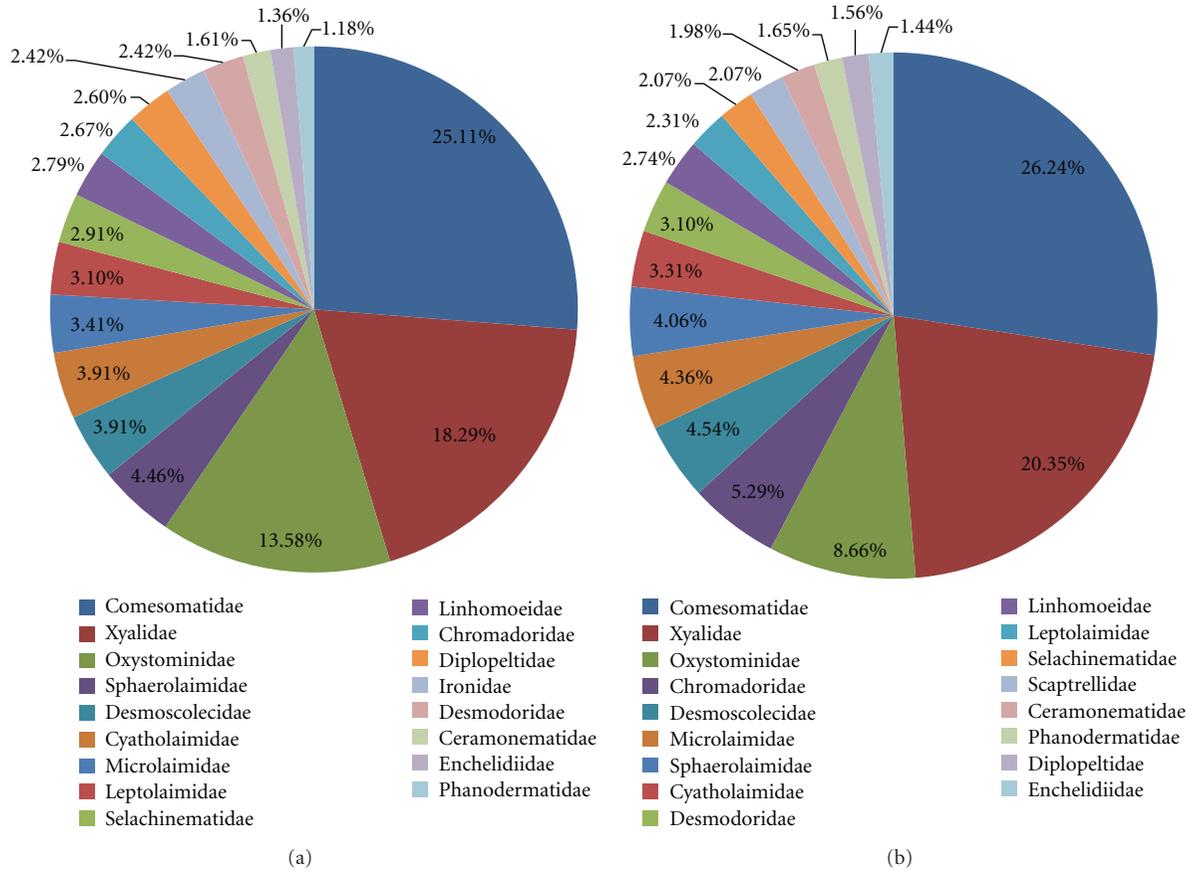


FIGURE 7: (a) Percent composition of nematode families in the western transect at dNGOM. (b) Percent composition of nematode families in the eastern transect at dNGOM.

more phylogenetic or functional diversity with increasing water depth [5]. The dominant taxa in the deep GOM were the family Comesomatidae and the genus *Sabatieria*. These taxa also dominated the shelf and slope communities of the Mediterranean but were less prominent in deeper sediments in that study [21]. The Comesomatid, *Cervonema*, was found in deeper sediments in our study and suggests that nematode assemblages are specific for certain habitats in the deep GOM. The other two dominant families in our study, Xyalidae and Oxystominidae, were also associated with deep-sea sediments in temperate slope regions [62]. The Chromadoridae and Monhysteridae are the dominant families and *Theristus* and *Acantholaimus* are the dominant genera in the deep North Atlantic [16].

4.3. *Functional Diversity.* At all stations, the trend of the regressions of feeding group with depth is similar to that of taxonomic and phylogenetic diversity measures and indicates that there were proportionally more higher order taxa in the deep sea and therefore proportionally more functional diversity in the community. Although the number of genera was lower at greater water depths, the number of families was represented equally. This pattern indicates that there was more evenness among feeding types in deeper waters. In other words, one particular type (1B or 1A) was

not dramatically dominant over the other two or three. This pattern also supports the observations of harpacticoid diversity [5] that in the deep GOM there are proportionally more higher order taxa and more phylogenetic or functional diversity. A study by Jensen [63] in the Norwegian Sea found that the deep sea fauna was dominated by deposit feeders and had few predators and scavengers. Deposit feeders were also the dominant group in the Puerto Rico trench and the Hatteras Abyssal plain [17]. Thistle and Sherman [16] found no evidence of feeding group correlation with environmental variables at 4625 m in the North Atlantic. Although, the proportion of predators and omnivores was low in the nematode meiofauna, their proportion was greater in nematodes collected in macrofauna [64]. Gambi et al. [65] suggested that the low prevalence of predatory and omnivorous nematodes in their study in the South Pacific Ocean may be attributed to the absence of freshly dead organisms.

4.4. *Cross-Taxon Spatial Variability.* The longitudinal east-west gradient observed in the similarity of genera found in the GOM is comparable to patterns found in other semienclosed basins such as the Mediterranean [24]. This gradient was not observed in the distribution of larger macrofauna taxa [44]. The latter occurred in four depth-related zones that stretched across the entire northern GoM

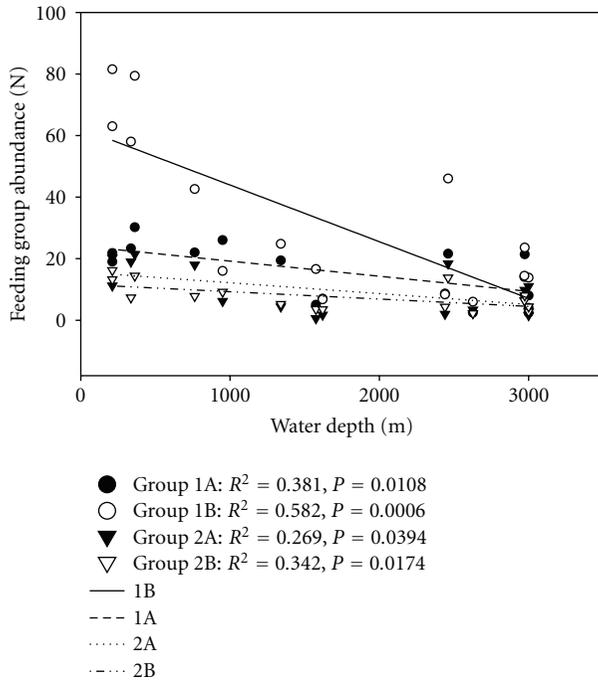


FIGURE 8: Regression of nematode feeding group abundances versus water depth in dNGOM. (1A nonselective deposit feeders; 1B selective deposit feeder; 2A epigrowth feeders; 2B omnivores and predators).

TABLE 5: SIMPER (Similarity Percentages) analysis of nematode feeding groups at GOM eastern and western transects (1A nonselective deposit feeders; 1B selective deposit feeder; 2A epigrowth feeders; 2B omnivores and predators).

Feeding group	Groups West and East		Average dissimilarity = 16.08
	Group West Av.Abund	Group East Av.Abund	
2A	1.92	2.21	36.68
1B	2.85	3.5	29.83
1A	2.67	2.92	19.29
2B	2.24	2.45	14.2

TABLE 6: Relationship between Nematoda, Harpacticoida, and Polychaeta spatial patterns. Values for the sample statistic (Rho) to test for matches in spatial patterns among stations and the significance probability level (P) for the match.

	Nematoda	Harpacticoida
Harpacticoida	Rho = 0.249 $P = 0.057$	—
Polychaeta	Rho = 0.028 $P = 0.408$	Rho = 0.159 $P = 0.170$

but with the two intermediate mid and deep slope zones being partitioned partially at intermediate longitudes. The similarity of the spatial pattern of nematode and harpacticoid copepods may be associated to their small size and dependence on similar food sources associated with detritus. The

input of organic matter from continental margins in the Gulf of Mexico contributes significantly to benthic productivity [66]. The sedimentation of particulate organic matter from phytoplankton production in the surface waters ranged from about $100 \text{ mg C m}^{-2} \text{ day}^{-1}$ down to ca. $5 \text{ mg C m}^{-2} \text{ day}^{-1}$ on the abyssal plain, based on sediment community oxygen demand [9, 67] and satellite observations of ocean color [42, 44]. Similar estimates, however, were not made on the western transect. The pattern of macro- and megabenthic species richness has also been related to food, habitat, pollution, and location in the Gulf of Mexico [68]. The lack of similarity between the distribution patterns of nematodes and polychaetes may be due to utilization of different food sources because some polychaete species are suspension/deposit feeders [69]. In addition, polychaetes are macrofauna and are less important in terms of total biomass and carbon cycling in deeper waters [9, 44]. Nematodes occur in high abundance and diversity and thus should be included in multitaxon studies of ecosystems for evaluation of broad biodiversity patterns. In summary, our results indicate significantly different nematode community composition between the western and eastern transects in the deep northern GOM that is consistent with broad patterns observed among other taxa.

5. Conclusions

Free-living nematodes are an abundant and diverse component of the meiofauna in the deep Gulf of Mexico. They follow the general trends of decreasing nematode abundance and diversity with increasing depth observed among other benthic taxa in the northern GOM along the continental shelf and in the deep sea. Divergence from this general bathymetric pattern may be attributed to bottom topography and interacting physical, biological, and chemical oceanographic processes. With the exception of selective deposit feeders that decreased with increasing water depth, the trophic diversity of nematodes was fairly even at all depths, indicating their significance as consumers at all depths. Finally, our analysis of nematode community structure and biodiversity in the dNGOM corroborates previous meiobenthic community investigations in this region. These data reinforce the notion that the dNGOM is a heterogeneous habitat where the Loop Current interacts with the Mississippi River outflow to strongly influence regional variations in meiobenthic community structure and function. The east-west gradient in nematode distribution shows congruence with other meiobenthic taxa but not with macrofauna, megafauna, and demersal fishes [44, 70].

Acknowledgments

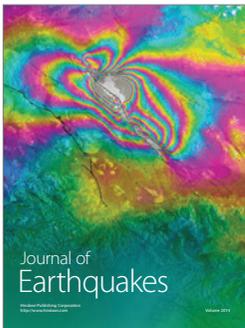
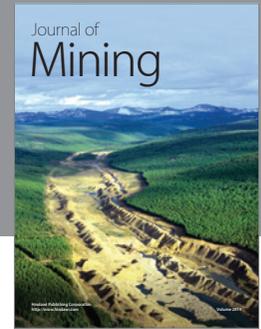
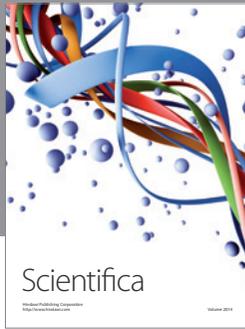
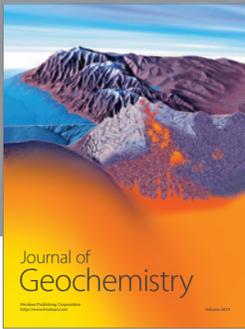
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