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Nematode assemblages of the northern Gulf of Mexico continental shelf

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Abstract.—This study examined free-living marine nematode assemblages of the northern Gulf of Mexico (GOM) continental shelf and their relationship to sediment characteristics. Sediment cores were collected in Fall 2012 and analyzed for trace metals, organic carbon, granulometry, and nematode genera. This study reports 100 genera of nematodes from 26 families, including 18 genera previously unreported in the GOM. A listing of the nematode diversity provides a bioinventory of nematodes on the GOM shelf. Cluster analysis, non-metric multidimensional scaling (nMDS) and principal component analysis revealed a distinction between eastern and western samples based on sediment characteristics as well as nematode assemblages. Spearman correlations revealed a significant correlation between sediment characteristics and nMDS coordinates, also suggesting that nematode assemblages have an east/west distinction that is reflective of their habitat. This study adds information on the biodiversity of marine nematodes, an abundant and diverse taxon from an area that is subject to anthropogenic disturbance.

Keywords: Benthic ecology, Biodiversity, Community composition, Continental shelf, Gulf of Mexico, Nematoda

Free-living nematodes are one of the most dominant metazoan groups in both biomass and abundance and are important consumers that contribute to benthic marine environments in many ways including oxygenation, bioturbation, and carbon cycling in marine sediments (Giere 2009). Nematodes are also extremely valuable in marine food webs, as they provide a critical food source for macrofauna and juvenile fishes (Danovaro et al. 2007, Giere 2009). While an estimated 4000–5000 marine nematode species have been named, the actual number of species present is thought to be significantly higher (Hope 2007). Therefore, documentation of

nematode taxa and an increased understanding of environmental factors influencing nematode distribution are needed in meiofauna research.

Numerous reports have documented the nematode genera from the Gulf of Mexico (GOM) from a variety of habitats including deep sea sediments (Sharma et al. 2012), shallow bays (Burgess et al. 2005), brine seeps (Jensen 1986), intertidal zones (Hopper 1961, Keppner 1986), and recently, the edge of the continental shelf (Landers et al. 2014). The latter report contributed nematode records for five locations near southeastern Louisiana and represents one of the few records of nematode taxa on the GOM shelf/slope. As the shelf is a relatively understudied

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area for nematode diversity and as the meiofauna community may be subject to anthropogenic disturbance, baseline studies of diversity are needed. This current study reports on nematode assemblages from an additional 16 shelf/slope collections extending from Louisiana to Florida, and examines the relationship of abiotic variables to those nematode assemblages.

Nematode distributions and assemblages are known to be significantly influenced by sediment characteristics such as sediment grain size, salinity, temperature, and particularly depth (Tietjen 1971, 1976, Soetaert & Heip 1995, Soetaert et al. 1995, Giere 2009, Sharma et al. 2011). A recent study of the northern Gulf of Mexico shelf/slope area reported two distinct sediment profiles that are related to the influence of the Mississippi River on shelf sediments (Martinec et al. 2014). This study is an extension of that research and aims to examine the relationship between sediment characteristics and nematode community structure. Given the two sediment profiles in the northern Gulf of Mexico sediments, the hypothesis for this work was that nematode assemblages in eastern sites (Florida and Alabama) will be distinct from those found in western sites (Louisiana and Mississippi), and that depth will correlate with nematode assemblage differences.

Materials and Methods

Sample collection.—Sediment samples were collected along the continental shelf and slope in the northern GOM in October and November 2012 from 49–361 m depths (Fig. 1), as described in Martinec et al. (2014). Samples were collected aboard the National Oceanic and Atmospheric Administration (NOAA) ship *Gordon Gunter* during their annual small pelagics fish survey. Collections were taken using a Shipek® grab, and five subcores (5 cm depth) from each grab were taken for

nematode community analysis (three subcores) and sediment analysis (two subcores) using a coring tube (inner diameter = 4.4 cm). The subcores for nematode analysis were immediately fixed in 5% formalin (final concentration) and the additional subcores remained unfixed and were refrigerated or frozen for sediment analysis. Global Positioning System coordinates and CTD data (e.g., conductivity, temperature, depth, and dissolved oxygen) for each site were provided by NOAA.

Sediment analysis.—The sediment data were used in a previous report and the methods are described in detail therein (Martinec et al. 2014). The raw data and metadata are publically available through the Gulf of Mexico Research Initiative Information and Data Cooperative (see acknowledgements). Briefly, sediments were analyzed for concentrations of 31 trace metals and organic carbon content at the Louisiana State University Agricultural Center following U.S. EPA Methods 200.7 and 9060, respectively (USEPA 1999, USEPA 2001). Granulometry was determined using a Geotech Sand Shaker Mechanical Sieve (Geotech Environmental Equipment, Denver, CO) at Jacksonville State University and divided into the following grain size categories: granules (>2 mm), very coarse+coarse sand (2 mm–500 µm), medium sand (500 µm–250 µm), fine sand (250 µm–125 µm), very fine sand (125 µm–63 µm), and silt+clay (<63 µm).

Nematode extraction and identification.—Formalin-fixed sediment samples were sieved (333 µm pre-sieve, followed by a 45 µm final sieve) and nematodes were extracted by Ludox® centrifugation (Burgess 2001). Total abundance was determined (Martinec et al. 2014) and the first 100 individuals from the pooled subcores from each site were identified to genus using standard identification keys based on morphological analysis (Platt & Warwick 1988, Smol et al. 2014). Nematodes were classified by feeding type based on buccal morphology either during genus identifi-

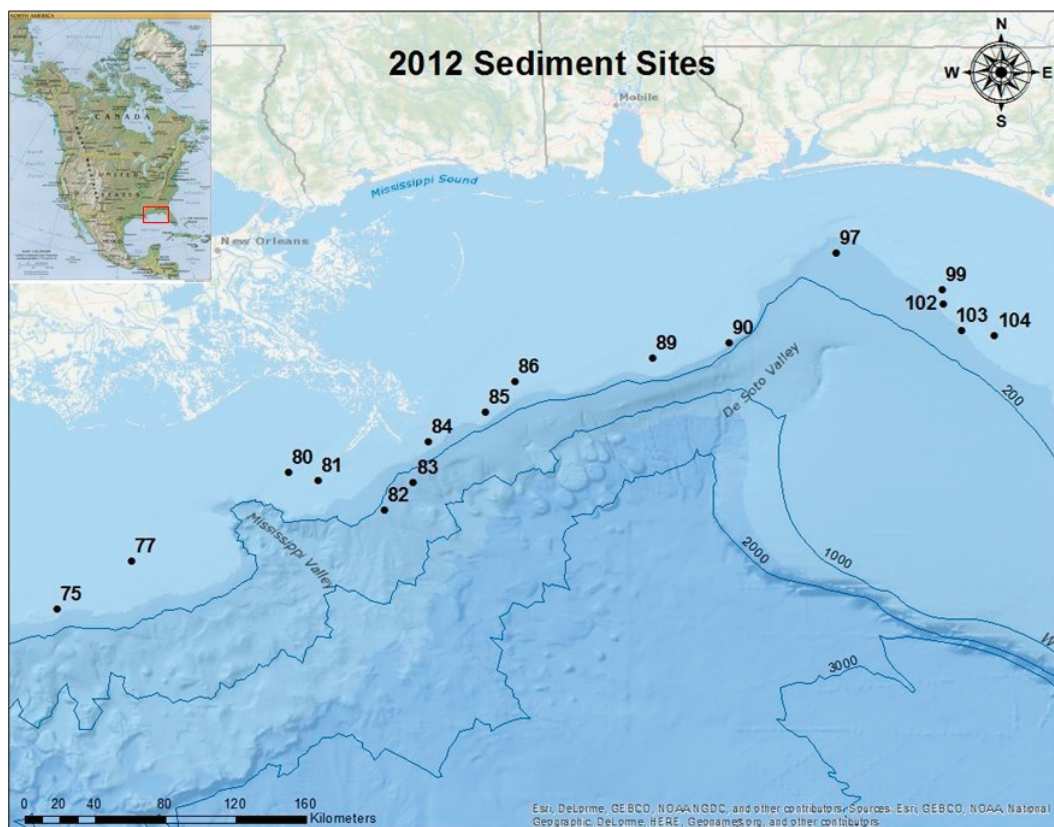


Fig. 1. Map of the 16 sediment sites for nematode assemblage analysis along the northern Gulf of Mexico continental shelf (depth contours in meters).

cation or from literature sources, using the classification of Wieser (1953). For some sites with few nematodes it was not possible to identify 100 individuals; therefore, sites with a minimum of 70 identified nematodes were used, which reduced the number of sample sites used in this manuscript to 16 (Table 1, Fig. 1). It has been shown that nematode community composition at the genus level reflects macro-ecological patterns (Soetart & Heip 1995, Vanaverbeke et al. 1997, Vanreusel et al. 2000, Fonseca & Soltwedel 2007) and thus provides an appropriate basis for comparisons of communities between habitats on a world-wide scale. Furthermore, identification of species is often based on adult male characteristics so juvenile and female identification cannot be confirmed.

Thus, identification to genus was used for community structure comparison. The subsampling of 100 nematodes from each location was determined mathematically valid for nematode community studies by Soetart & Heip (1990). Urban-Malinga et al. (2006) provided a good explanation of this sampling strategy in a study of Baltic and North Sea nematode communities.

Data analysis.—Biological indices including richness (S) and the Shannon-Wiener diversity index H' (\log_e) were calculated using PRIMER[®] software (Version 6) (Table 2) (Clarke and Gorley 2006). PRIMER[®] was also used for cluster analysis, non-metric multidimensional scaling (nMDS), and principal component analysis (PCA). Data were analyzed for general trends using SPSS[®] software (Ver-

Table 1.—Nematode genera and families identified at 16 sites along the northern Gulf of Mexico (GOM) continental shelf, including 18 new GOM records (***). Feeding types represent selective deposit feeders (1A), non-selective deposit feeders (1B), epistrate feeders (2A), and predators/omnivores (2B).

Family	Genus	New	Feed	Site																Tot.
				75	77	80	81	82	83	84	85	86	89	90	97	99	102	103	104	
Aegialoalaimidae	<i>Cyartonema</i>		1A										1	3						4
	<i>Aegialoalaimus</i>		1A											5	2			1		8
	<i>Diplopeltoides</i>		1A					2	1						1					4
	<i>Rhabdocoma</i>		1A					3												3
Axonolaimidae	<i>Axonolaimus</i>		1B	1		2		1			1		1							6
	<i>Odontophora</i>		1B		1		4	16				1	5	2				1	4	34
Ceramonomatidae	<i>Pselionema</i>		1A	20	1					2	2	1	6	7	5	3	8	1	1	57
	<i>Ceramonema</i>		1A														1			1
	<i>Dasyneumella</i>		1A													1				1
Chromadoridae	<i>Chromadora</i>		2A				1	1		3										5
	<i>Chromadorita</i>		2A			2														2
	<i>Chromadorina</i>		2A		1															1
	<i>Dichromadora</i>		2A		2										4	1				7
	<i>Endeolophos</i>	***	2A	1	1			2	2		1	1	1		1					10
	<i>Graphonema</i>	***	2A	1															1	2
	<i>Prochromadorella</i>		2A														1			1
	<i>Ptycholaimellus</i>		2A		2															2
	<i>Spilophorella</i>		2A				1													1
	<i>Cervonema</i>		1A	2			1	6	10			3	1	1	13	1	1	3	8	50
Comesomatidae	<i>Comesoma</i>		1B										4							4
	<i>Dorylaimopsis</i>		2A	7	26	30	36	1		11	9	20	3		2	10	11	25	5	196
	<i>Hopperia</i>		2B	11	1		1	4	8	3	10			4	5			2		49
	<i>Laimella</i>		1A					2	5				1	1						9
	<i>Paramesonchium</i>		2B								2									2
	<i>Pierrickia</i>	***	1B					1												1
	<i>Sabatieria</i>		1B	7	7	2	16	13	4	8	9	5			7	18	6	16	4	122
	<i>Vasostoma</i>	***	1B																1	1
	<i>Maryllynia</i>		2A	2	3	4	4			16	1				1	1				32
	<i>Cyatholaimus</i>		2A														1		1	2
Cyatholaimidae	<i>Longicyatholaimus</i>		2A		1	4	1	1	2			5	1	1				1	2	19
	<i>Paracanthonchus</i>		2A	1																1
	<i>Paracyatholaimus</i>		2A									1								1
	<i>Pomponema</i>		2A										3							3
	<i>Desmodora</i>		2A	4	2	3		3	5	1	3	2	5	2	5	3	3		3	44
	<i>Acanthopharyngoides</i>		2A																	2
Desmodoridae	<i>Chromaspirina</i>		2A								3		1	2	3					7
	<i>Desmodorella</i>		2A													2	2			4
	<i>Echinodesmodora</i>	***	2A									8	1	2						11
	<i>Eubostrichus</i>		1A										2							2
	<i>Metachromadora</i>		2A															1		1
	<i>Molgolaimus</i>		2A				7	1			2		8	1						19
	<i>Parallelocoilas</i>	***	2A														1			1
	<i>Spirinia</i>		1A	2	3	2	2	1	4	1	2	2	4			10	3	2	10	48
	<i>Desmoscolex</i>		1A	4	1			1	1				6	1	3	6	2		3	28
	<i>Desmolorenzia</i>	***	1A																1	1
Desmoscolecidae	<i>Quadricoma</i>		1A	1	5	5	5		3	13			2	5	2	2	1		2	46
	<i>Tricoma</i>		1A	10	5	5	2		3	4	1	5	7	8	13	1	7	1	3	75
	<i>Campylaimus</i>		1A						2		1			3						6
	<i>Diplopeltula</i>		1A				1		2				1	1	1	1		1		8
Epsilonematidae	<i>Perepsilonema</i>	***	1A								2									2
Ironidae	<i>Thalassironus</i>		2A		1															1

Table 1.—Continued.

Family	Genus	New	Feed	Site																Tot.
				75	77	80	81	82	83	84	85	86	89	90	97	99	102	103	104	
Leptolaimidae	<i>Antomicron</i>		1A	2	1						1	1			2					7
	<i>Alaimella</i>		1A										1					1		2
	<i>Camacolaimus</i>		2A				1			8		7								16
	<i>Leptolaimus</i>		1A	2	2	4		2	1		3	2	2		1	1		1		21
	<i>Procamacolaimus</i>	***	1A									3								3
Linhomoeidae	<i>Disconema</i>		1B														1			1
	<i>Linhomoeus</i>		1B					1						1		1				3
	<i>Megadesmolaimus</i>	***	1B													1				1
	<i>Metalinhomoeus</i>		1B					2	4			2	1							9
	<i>Paralinhomoeus</i>		1B							1										1
	<i>Terschellingia</i>		1A			25	12	5	11	12	18	1			2	1	2	2		91
	<i>Bolbolaimus</i>		2A	2	14	2					1	2	1	1			6	1		30
Microlaimidae	<i>Aponema</i>	***	2A		1								1				1			3
	<i>Microlaimus</i>		2A	1	1	2	1	9	5	1	3	2	2	4	1	2			2	36
	<i>Molgolaimus</i>		2A		1															1
Monhysteridae	<i>Monhystera</i>		1B					3	5	1			1							10
Neotonchidae	<i>Neotonchus</i>		2A						1				1	2						4
Oncholaimidae	<i>Oncholaimellus</i>		2B														1			1
Oxystominidae	<i>Halalaimus</i>		1A	1	1	1		1	2		2		1		3	2	1			15
	<i>Nemanema</i>		1A				2													2
	<i>Oxystomina</i>		1A		2		1	1	1	6	2						1			14
Paramicrolaimidae	<i>Paramicrolaimus</i>		2A													1	3	4		8
Phanodermatidae	<i>Phanodermopsis</i>		1A										2							2
Selachinematidae	<i>Cheironchus</i>		2B			3					1	3		3	2	3	3	1	2	21
	<i>Gammanema</i>		2B		1	2		2												5
	<i>Halichoanolaimus</i>		2B			1		2	1		1	3			2			1	11	11
	<i>Latronema</i>	***	2B											9		2		11		22
	<i>Richtersia</i>		2A	6	2						1	3	4	13	3	4	6	5	1	48
	<i>Synonchiella</i>		2B	1												3	2	1	1	8
	<i>Siphonolaimus</i>		1A							3				1		3		1	1	9
Siphonolaimidae	<i>Parastomonema</i>	***	1A															3		3
Sphaerolaimidae	<i>Doliolaimus</i>	***	2B			1	1													2
	<i>Sphaerolaimus</i>		2B	1	5		1	2	1	2	1	1			5	4	2			25
	<i>Subsphaerolaimus</i>	***	2B												2			1		3
Tarvaiidae	<i>Tarvaia</i>		1A										2	3	2	1	1			9
Thoracostomopsidae	<i>Mesacanthoides</i>		2B													1				1
Trefusiidae	<i>Halanonchus</i>	***	1B									2								2
	<i>Rhabdocoma</i>		1B		1															1
Xyalidae	<i>Daptonema</i>		1B			4	3	1	6	1	10		6	1	1				1	34
	<i>Ammotheristus</i>		1B								2									2
	<i>Amphimonhystrella</i>		1B		2															2
	<i>Elzalia</i>		1B	1				1								3	2			7
	<i>Gonionchus</i>		1B											1						1
	<i>Monhysteroides</i>	***	1B			1		2	2		2	4		2	2	5	1			21
	<i>Paramonhystera</i>		1B	1	1		4	2		4	3	1			3	2				21
	<i>Promonhystera</i>	***	1B			1				6										7
	<i>Rhynchonema</i>		1B										1							1
	<i>Scaptrella</i>		1B										1					1		2
	<i>Theristus</i>		1B					1			1		1					2		5
	<i>Stylotheristus</i>		1B											1						1
TOTALS			1A	44	21	42	26	22	46	45	32	19	46	33	48	33	28	14	32	531
	Feeding types		2A	26	57	47	52	18	15	41	24	53	28	28	21	24	35	36	25	530
			1B	10	12	10	27	43	29	14	28	19	17	8	13	30	10	17	13	300
			2B	13	7	7	3	10	10	5	15	7	0	16	16	13	8	5	15	150

Table 1.—Continued.

Family	Genus	New	Feed	Site																Tot.
				75	77	80	81	82	83	84	85	86	89	90	97	99	102	103	104	
	Total individuals			93	97	106	108	93	100	105	99	98	91	85	98	100	81	72	85	1511
	Total genera			26	30	22	23	31	30	21	30	29	35	29	30	32	29	21	29	101
	Total families			13	15	13	13	15	17	14	15	15	18	15	16	16	14	13	11	26

sion 12.0.1). Maps were created using ArcGIS (version 10.2.2).

Results

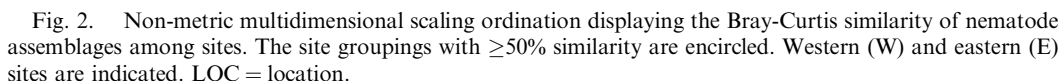
Nematode assemblages.—This study examined 1511 nematodes in total of which 100 genera from 26 families were identified (Table 1). Eighteen of these genera were not found in previously published checklists for the GOM. The richest family for all genera was Xyalidae (number of genera, S = 12), followed by Desmodoridae (S = 10), Chromadoridae (S = 9) and Comesomatidae (S = 9). The most overall abundant families were Comesomatidae (28.7% of total abundance), Desmoscolecidae (9.9%), Desmodoridae (9.8%), Sela-

chinematidae (7.6%), Linhomoeidae (7.0%), and Xyalidae (6.9%). The most abundant genera were *Dorylaimopsis* (13%), *Sabatieria* (8.1%), *Terschellingia* (6.0%), *Tricoma* (4.9%) and *Pselionema* (3.8%). Site 89 had the highest richness (S) and diversity (H’); site 103 had the lowest H’ and was tied with site 84 for the lowest S. Richness ranged from 21–35 genera, and H’ ranged from 2.25–3.27. (Table 2).

Of the four feeding group categories for free-living nematodes, the dominant groups were selective deposit feeders (1A) (35.1%) and epistrate feeders (2A) (35.1%), while non-selective deposit feeders (1B) (19.9%) and scavengers/predators (2B) (9.9%) were less common. All four feeding groups were represented in the list of new GOM records (Table 1).

Table 2.—Summary of site data and nematode diversity indices from each site. S = genus richness, H’ = Shannon-Wiener diversity index.

Site	Latitude	Longitude	Depth (m)	S	H’
75	28.12458	–90.89370	113.2	26	2.74
77	28.36875	–90.51224	49.3	30	2.76
80	28.82299	–89.71073	69.7	22	2.43
81	28.78352	–89.56122	87.5	23	2.38
82	28.63315	–89.22120	242	31	2.98
83	28.77422	–89.07505	360.8	30	3.13
84	28.98084	–88.99902	84.8	21	2.67
85	29.13242	–88.70763	86.1	30	2.93
86	29.28921	–88.55590	65.7	29	3.00
89	29.40838	–87.85597	74.4	35	3.27
90	29.48278	–87.46487	85.3	29	3.01
97	29.94476	–86.91794	150.9	30	3.08
99	29.75450	–86.37698	102.3	32	3.04
102	29.68343	–86.36935	114.1	29	3.03
103	29.54796	–86.27860	123.8	21	2.25
104	29.52271	–86.11068	81.3	29	3.03
Min			49.3	21	2.25
Max			360.8	35	3.27
Mean			118.2	28	2.86



Principal component analysis.—Principal component analysis based on trace metals and particle size distribution of sediments demonstrated two obvious site clusters (Fig. 3). Principal components (PCs) 1–2 (Table 3) accounted for 79.7% of cumulative variation in the dataset. The PC1 axis contained a slightly stronger contribution from the trace metals than did granulom-

Spearman correlations.—Coordinates from non-metric multidimensional scaling (nMDS) of nematode assemblages showed significant Spearman's rank correlations with PC scores (trace metals and granulometry) (Table 4), individual trace metals, particle size categories, organic carbon percentages, longitude, and nematode den-

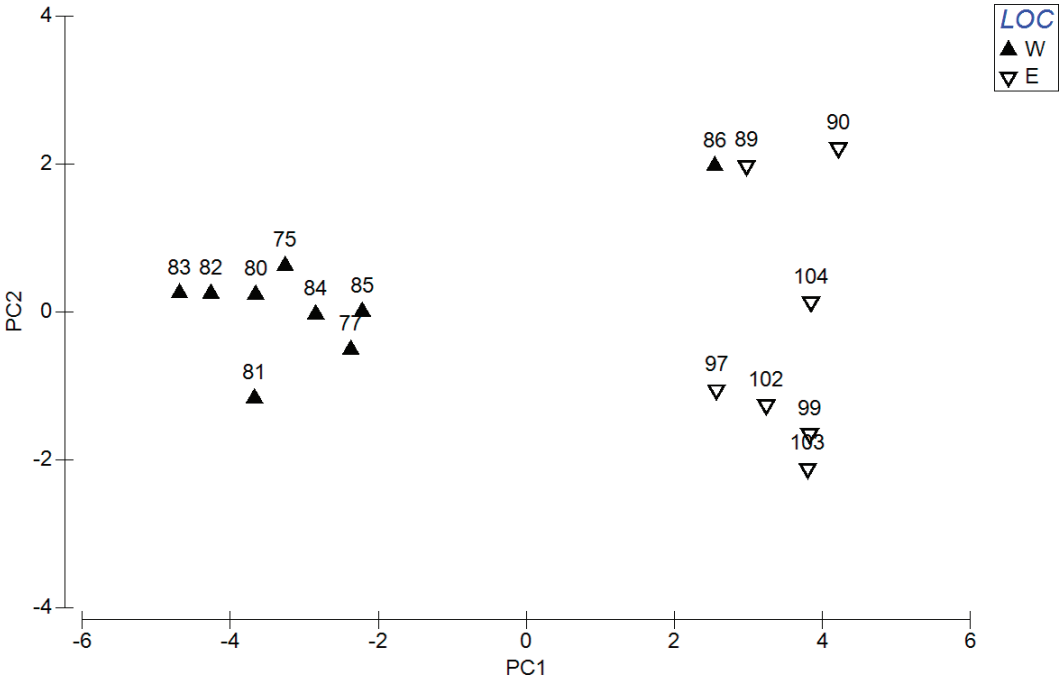


Fig. 3. Principal component analysis ordination of trace metals and granulometry data from sites. Two distinct sediment zones are revealed, eastern (E) and western (W) locations (LOC). Site 86 was a transition site between the two sediment zones but grouped with the eastern sites.

Table 3.—Results from PCA of trace metals and granulometry, showing the eigenvectors or groups of variables constituting each principal component (PC) that explained the highest percentage of the total variation in the data.

Variable	Eigenvectors	Eigenvectors
	PC1	PC2
Al	−0.279	0.014
Fe	−0.277	0.045
Pb	−0.278	−0.002
Ni	−0.278	−0.055
Ba	−0.213	0.095
Cr	−0.272	−0.080
Cu	−0.273	−0.126
V	−0.277	0.065
Zn	−0.279	0.007
Ca	0.248	−0.184
Sr	0.249	−0.210
Granules	−0.165	0.049
V coarse/coarse	−0.144	0.184
Med sand	0.143	0.625
Fine sand	0.216	0.116
Very fine sand	0.185	−0.539
Silt/clay	−0.151	−0.194
Org C	−0.218	−0.336

sity. These correlations suggest that nematode assemblages also follow an east/west pattern as do the sediment characteristics. No correlation was found between nMDS scores and depth or Shannon-Weiner diversity indices.

Nematode feeding groups.—All four of the nematode trophic groups were represented at each site, with the exception of site 89 that had no omnivores/predators (Fig. 4). Spearman analysis of the percentages of each trophic group revealed a negative correlation with group 2A (epistrate feeders) and depth. When western and eastern sites were analyzed separately, a strong negative correlation was present between group 2A and depth in the west (Fig. 5) but no correlation occurred in the east. Group 2A also had a negative correlation with coarse sediment in the west, as coarse sediment increased with depth. A consequence of the declining percentage of group 2A with depth in the

Table 4.—Correlation analysis (Spearman’s rho) between nMDS coordinates of nematode assemblages, principal component scores (PC) of trace metals and granulometry, trace metals, granulometric data, longitude and depth. Trace metals are represented by Al, Ca, and Sr, as all other metals were highly correlated with these three. *p < 0.05, **p < 0.01, ***p < 0.001

Variable	nMDS1	nMDS2
PC 1	−0.868***	−0.159
PC 2	−0.380	0.774***
Al	0.885***	0.191
Ca	−0.882***	−0.100
Sr	−0.879***	−0.191
Granules	0.556*	0.334
Fine sand	−0.715**	−0.106
Very fine sand	−0.524*	−0.644**
Silt/clay	0.626**	−0.332
Org Carbon	0.815***	−0.032
Longitude	0.753**	−0.135
Depth	0.006	−0.150
Nematode density	0.541*	−0.129

west was an increasing percentage of deposit feeders (1A + 1B) with depth, which was statistically significant. In the east, group 1A (selective deposit feeders) correlated positively with granules and negatively with very fine sand, though there was no relationship to depth.

Discussion

This study documents nematode assemblages found at 16 locations along the northern GOM shelf/slope habitat, an assemblage that has only been reported once before in a preliminary study (Landers et al. 2014). In that earlier study, nematodes from five box cores collected on the same cruise as the current study were reported. A direct comparison of sites 81, 82, 84, 85, and 86 from that study with the Shipek® grabs made in parallel for this report provided further insight into the

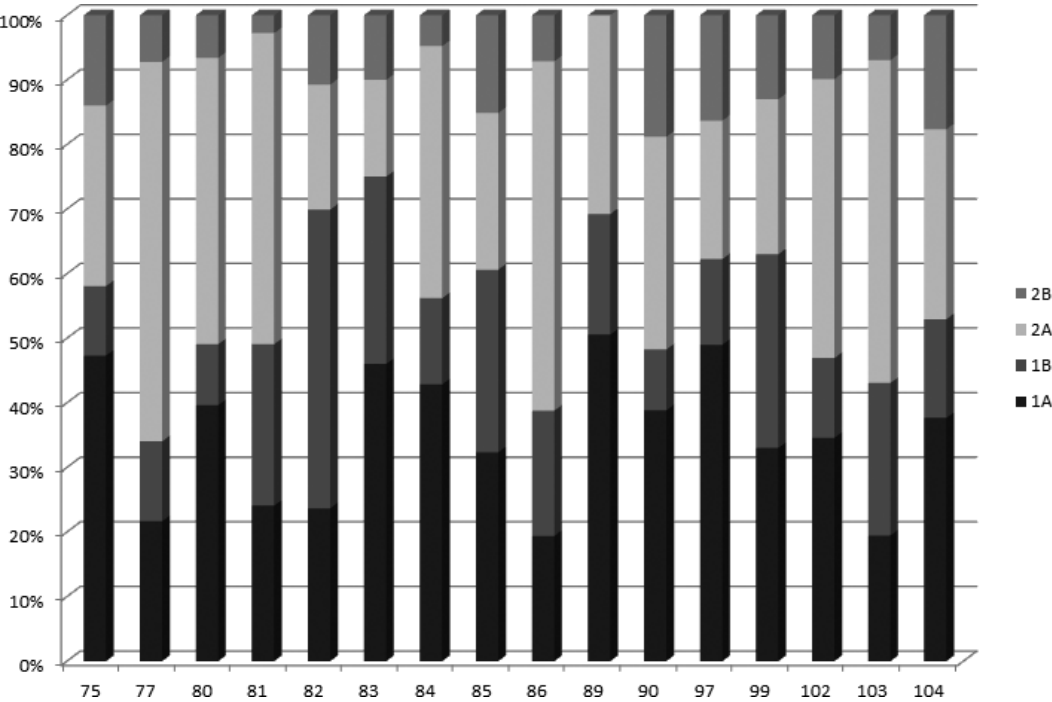


Fig. 4. Percentage of nematodes from each feeding group, from each site. 1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A = epistrate feeders, 2B = omnivores/predators.

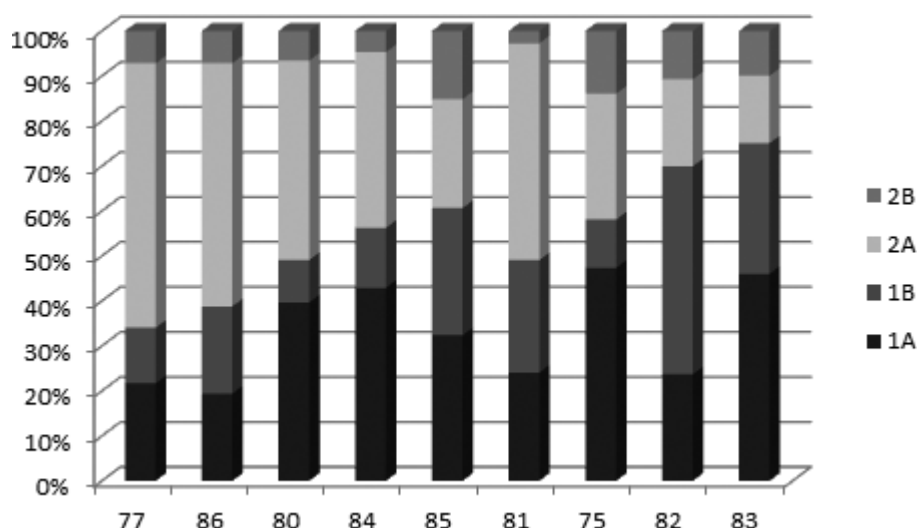


Fig. 5. Percentage of nematodes from each feeding group, from each western site, presented from left to right with increasing depth.

Gulf nematode fauna, as it illustrated the patchiness of nematode distribution at similar sites. Twenty-three genera noted from those five sites in this current report were not observed in the earlier report from the five box cores, and twenty-four genera reported from the box cores were not observed in the current study. Though the box core nematodes were isolated using a larger final sieve (63 μm) this would exclude mostly the smaller juveniles from the study compared to the 45 μm sieve. The upper sieve size (333 μm) is more important, and was used for both the box core and Shipek® collections. The differences between the collections suggest a high nematode diversity in the Gulf sediments. The current report now documents 18 genera as new records for the GOM when compared to available checklists (King 1962, Jensen 1986, Burgess et al. 2005, Hope 2009, Sharma et al. 2012, Landers et al. 2014). Numerous genera revealed a distinct east or west preference (Table 1), which is most likely a reflection of sediment grain size characteristics.

Our hypothesis that nematode assemblages would differ when eastern and western sites were compared was support-

ed by this study. Cluster analysis revealed a $\geq 50\%$ similarity among all western sites (plus site 97), along with three other clusters in the east (sites 89, 90, 104; sites 99, 102; site 103) that were $\geq 50\%$ similar within each group. In addition to nematode communities revealing an east versus west pattern, abundance data and organic carbon correlated positively with nMDS1 scores, following higher nematode densities in the west. Similarly, abundance data from all 26 original Shipek® sites (Martinec et al., 2014) were shown earlier to correlate positively with sediment aluminum and negatively with sediment calcium, indicating a similar trend.

The east/west nematode assemblage pattern was supported by significant Spearman correlations between nMDS coordinates and trace metals, and between nMDS coordinates and sediment grain size characteristics that define the eastern and western study area. An earlier report from this research (Martinec et al. 2014) documented two distinct sediment zones in the northern GOM, one to the west of site 86 and one to the east. The sediment zone to the west was dominated by aluminosilicate minerals attributable to Mississippi River

outflow, and contained higher levels of Al, Ba, Cr, Cu, Fe, Ni, Pb, V, Zn, and organic carbon when compared to sediment from the eastern zone, where Ca and Sr were high due to the carbonate sediment. The current study strongly supports these earlier findings using PCA that combines trace metal data with sediment grain size data, as those two factors are known to be linked (Holmes 1973, McGowen et al. 1979, Wade et al. 2008). Interestingly, the PCA of sediment characteristics matches the trend observed with multi-dimensional scaling of nematode communities. Principle component 1 separated sites based on stronger contributions of trace metals and organic carbon rather than granulometry, which effectively separates eastern and western sites. Principle component 2 separated sites with more input from granule size distribution on the Y-axis. Thus, western sites with more homogeneous sediment were not separated by PC2, whereas the Florida sites were separated. This same pattern was reflected in the nMDS of nematode communities. All of the western sites grouped with a $\geq 50\%$ similarity but the eastern sites did not all group together, revealing how nematode communities can reflect sediment differences and vice-versa.

The most abundant genera observed in this study (*Dorylaimopsis*, *Sabatieria*, and *Terschellingia*) have been linked to fine sediments or sands, depending on the species (Armenteros et al. 2009, Jensen 1981, Tietjen 1976, 1977, Vincx et al. 1990). In this study, *Sabatieria* correlated with fine sediments (positive correlation with silt+clay and negative correlation with medium sand), while *Terschellingia* and *Dorylaimopsis* showed no correlations with sediment granulometry, suggesting that individual genera are likely influenced by a number of factors. No correlations were found with feeding groups and sediment grain size except for very coarse/coarse sediment, which correlated

positively with group 1A and negatively with group 2A.

Numerous earlier reports established that depth is a major factor that influences nematode assemblages and density (e.g. Soetaert & Heip 1995, Soetaert et al. 1995, Coull et al. 1982, Netto et al. 2005, Sharma et al. 2011, Tietjen 1971), and specifically that nematode feeding type diversity regresses with depth (Sharma et al. 2012). The study by Sharma et al. (2012) from the Gulf of Mexico examined sites with significant depth variation, extending from the continental shelf to the deep communities with a depth range of 212–3000 m. Our results did not support a relationship between depth and nematode assemblage nMDS coordinates, though one of the nematode feeding types (2A- epistrate feeders) had a significant negative correlation with depth. Epistrate feeders are thought to primarily graze on diatoms and other microalgae (Moens et al. 2014), a food source that would be less available with increasing depth. When eastern and western sites were analyzed separately, the western locations revealed a strong correlation with decreasing epistrate feeders (primarily a decrease in the genus *Dorylaimopsis*), and increasing deposit feeders (1A + 1B) with depth. This pattern of decreasing epistrate feeders and increasing deposit feeders with greater depth was reported in North Carolina, though the change in feeding groups did not occur until 500–600 m in depth (Tietjen 1971). No feeding group correlations were significant with depth in the east. It is possible that such a difference exists because of greater homogeneity of the sediment in the west, which allowed a single variable such as depth to reveal its importance statistically. In the east, with more heterogeneous sediment characteristics, a depth effect was not revealed.

Site 103 contained the lowest richness (tied with site 84) and diversity of all sites, and was an isolated group in the nMDS ordination and cluster analysis (which may

be a reflection of the lower number of animals identified at that site). This site was dominated by *Dorylaimopsis* (34.7%) and *Sabatieria* (22.2%). Site 103 also bordered the continental slope and contained a very different sediment composition than surrounding sites, with the highest percentage of silt + clay and very fine sand of any of the eastern sites. Therefore, the organisms at this site could be influenced by fine sediments, as there was no substantial increase in trace metals or organic carbon at this site. Another site that had an unusual nMDS grouping with others was site 97, in the northern DeSoto Valley, which clustered with all of the western sites. This site was, however, the deepest collection site of the Florida sites and had a high organic carbon concentration, more similar to those found in western sediments. Site 86 grouped with western nematode assemblages but grouped with eastern sites using PCA of sediment characteristics. This site is very close to the transition between the two sediment profiles reported by Martinec et al. (2014) and is likely not as strongly influenced by Mississippi River outflow as the other western sites.

Overall, the biotic index values (S and H') for sites in this study were comparable to other studies (e.g., Hua et al. 2014, Gambi et al. 2003, Moreno et al. 2008, Netto et al. 2005). Sites in the current study contained relatively low concentrations of most trace metals (below NOAA aquatic-life benchmarks and EPA chronic-exposure benchmarks for sediment contamination) (Nowell et al. 2013). They also contained low levels of organic carbon when compared to oiled sediment (Natter et al. 2012), as well as low PAH concentrations determined from a previous report (Landers 2014, Martinec et al. 2014). Trace metal concentrations were useful to this study as they are known to correlate with sediment granulometry, but were not thought important with regards to toxic effects. Overall, the

sediments of the continental shelf appeared to have relatively low levels of detectable pollution, even in regards to the Deepwater Horizon oil spill and ongoing anthropogenic incidents in the Gulf of Mexico.

Conclusions

This study documents the nematode fauna of the Gulf of Mexico continental shelf and reports 18 new Gulf of Mexico genus records. The nematode assemblages reveal an east/west pattern, which correlates with characteristics that distinguish sediments in Florida and Louisiana. The most significant factor that influenced nematode assemblages appeared to be sediment grain size, which was associated with varying organic carbon content and concentrations of trace metals.

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Literature Cited

- Armenteros, M., A. Ruiz-Abierno, R. Fernández-Garcés, J.A. Pérez-García, L. Díaz-Asencio, M. Vincx, & W. Decraemer. 2009. Biodiversity patterns of free-living marine nematodes in a tropical bay: Cienfuegos, Caribbean Sea. *Estuarine, Coastal and Shelf Science* 85, 179–189.

- Burgess, R., 2001. An improved protocol for separating meiofauna from sediments using colloidal silica sols. *Marine Ecology Progress Series* 214, 161–165.
- Burgess, R., J. Sharma, R.S. Carr, & P. Montagna. 2005. Assessment of storm water outfalls in Corpus Christi Bay, Texas, USA using meiofauna. *Meiofauna Marina* 14, 157–169.
- Clarke, K.R., & R.N. Gorley. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth, United Kingdom.
- Coull, B.C., Z. Zo, J.H. Tietjen, & B.S. Williams. 1982. Meiofauna of the southeastern United States continental shelf. *Bulletin of Marine Science* 32, 139–150.
- Danovaro, R., M. Scopa, C. Gambi, & S. Frascchetti. 2007. Trophic importance of subtidal metazoan meiofauna: Evidence from *in situ* exclusion experiments on soft and rocky substrates. *Marine Biology* 152, 339–350.
- Fonseca, G., & T. Soltwedel. 2007. Deep-sea meiobenthic communities underneath the marginal ice zone off Eastern Greenland. *Polar Biology* 30, 607–618.
- Gambi, C., A. Vanreusel, & R. Danovaro. 2003. Biodiversity of nematode assemblages from deep-sea sediments of the Atacama Slope and Trench (South Pacific Ocean). *Deep-Sea Research I* 50, 103–117.
- Giere, O., 2009. *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments*, 2nd edition, Springer, Berlin, Germany.
- Holmes, C.W. 1973. Distribution of selected elements in surficial marine sediments of the northern Gulf of Mexico continental shelf and slope. U.S. Government Printing Office, Washington, DC, USA.
- Hope, W.D. 2007. Nematoda, Pp. 234–266 in J.T. Carlton, ed., *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon*, 4th edition, The University of California Press, Richmond, CA, USA. 1001 pp.
- Hope, W. D. 2009. Free-living marine Nematoda of the Gulf of Mexico, Pp. 1111–1123 in D.L. Felder, D.K. Camp, eds., *Gulf of Mexico, Origin, Waters, and Biota*. Vol. 1, Biodiversity, Texas A&M University Press, College Station, Texas, USA. 1393 pp.
- Hopper, B. 1961. Marine nematodes from the coast line of the Gulf of Mexico. *Canadian Journal of Zoology* 39, 183–199.
- Hua, E., Z. Zhang, H. Zhou, & X. Liu. 2014. Biodiversity of free-living nematodes in the Yangtze River estuary and its adjacent waters. *Proceedings of the Biological Society of Washington* 127, 23–34.
- Jensen, P. 1981. Species distribution and a microhabitat theory for marine mud dwelling Comesomatidae (Nematoda) in European waters. *Cahiers de Biologie Marine* 22, 231–241.
- Jensen, P. 1986. Nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. IV. Ecological Aspects. *Marine Biology* 92, 489–503.
- Keppner, E.J. 1986. New species of free-living nematodes (Nematoda:Enoplidae) from Bay County, Florida, USA. *Transactions of the American Microscopical Society* 105, 319–337.
- King, C.E. 1962. Some aspects of the ecology of psammolittoral nematodes in the northeastern Gulf of Mexico. *Ecology* 43, 515–523.
- Landers, S.C., A.C. Nichols, N.K. Barron, C.A. Schimmer, R. Tao, K. Yu, P.M. Stewart, & E. Ólafsson. 2014. Nematode and copepod diversity (2012) from Louisiana near the Deepwater Horizon oil spill. *Proceedings of the Biological Society of Washington* 127(1), 47–57.
- Martínez, C.C., J.M. Miller, N.K. Barron, R. Tao, K. Yu, P.M. Stewart, A.C. Nichols, D.A. Steffy, & S.C. Landers. 2014. Sediment chemistry and meiofauna from the northern Gulf of Mexico continental shelf. *International Journal of Oceanography* 2014, e625718, <http://dx.doi.org/10.1155/2014/625718>.
- McGowen, J.H., J.R. Byrne, & B.H. Wilkinson. 1979. *Geochemistry of Bottom Sediments-Matagorda Bay System*. University of Texas at Austin, Bureau of Economic Geology Circular 79-2, Austin, TX, USA.
- Moens, T., et al. 2014. Ecology of free-living marine nematodes. In: Schmidt-Rhaesa, A. (Ed.). *Handbook of Zoology, Volume 2. Nematoda*. De Gruyter, Berlin, 109–152.
- Moreno, M., L. Vezzulli, V. Marin, P. Laconi, G. Albertelli, & M. Fabiano. 2008. The use of meiofauna diversity as an indicator of pollution in harbours. *ICES Journal of Marine Science* 65(8), 1428–1435.
- Natter, M., J. Keesen, Y. Wang, A.R. Keimowitz, B.C. Okeke, A. Son, & M. Lee. 2012. Level and degradation of Deepwater Horizon spilled oil in coastal marsh sediments and pore-water. *Environmental Science and Technology* 46(11), 5744–5755.
- Netto, S.A., F. Gallucci, & G.F.C. Fonseca. 2005. Meiofauna communities of continental slope and deep-sea sites off SE Brazil. *Deep-Sea Research I* 52, 845–859.
- Nowell, L.H., A.S. Ludtke, D.K. Mueller, & J.C. Scott. 2013. Organic contaminants, trace and major elements, and nutrients in water and sediment sampled in response to the Deepwater Horizon oil spill. U.S. Geological Survey

- Open File Report 2012-5228, U.S. Geological Survey, Reston, VA, USA.
- Platt, H.M., & R.M. Warwick. 1988. Free-living marine nematodes. Part II. British Chromadorids. Synopses of the British Fauna (New Series) vol. 38, E.J. Brill/Dr. W. Backhuys, Leiden. 502 pp.
- Sharma, J., J.G. Baguley, B.A. Bluhm, & G.T. Rowe. 2011. Do Meio- and Macrobenthic nematodes differ in community composition and body weight trends with depth? *PLoS ONE* 6(1):e14491. Doi:10.1371/journal.pone.0014491.
- Sharma, J., J.G. Baguley, P.A. Montagna, & G.T. Rowe. 2012. Assessment of longitudinal gradients in nematode communities in the deep northern Gulf of Mexico and concordance with benthic taxa. *International Journal of Oceanography* 2012, e903018, <http://dx.doi.org/10.1155/2012/903018>.
- Smol, N., A. Muthumbi, & J. Sharma. Order Enopla. In Schmidt-Rhaesa, A. (Ed.) 2014. *Handbook of Zoology, Volume 2: Nematoda*. De Gruyter, Berlin, 193–249.
- Soetaert, K., & C. Heip. 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. *Marine Ecology Progress Series* 59, 305–307.
- Soetaert, K., & C. Heip. 1995. Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. *Marine Ecology Progress Series* 125, 171–183.
- Soetaert, K., M. Vincx, & C. Heip. 1995. Nematode community structure along a Mediterranean shelf-slope gradient. *Marine Ecology* 16, 189–206.
- Tietjen, J.H. 1971. Ecology and distribution of deep-sea meiobenthos off North Carolina. *Deep-Sea Research* 18, 941–957.
- Tietjen, J.H. 1976. Distribution and species diversity of deep-sea nematodes off North Carolina. *Deep-Sea Research* 23, 755–768.
- Tietjen, J.H. 1977. Population distribution and structure of the free-living nematodes of Long Island Sound. *Marine Biology* 43, 123–136.
- Urban-Malinga, B., S.I.C. Hedtkamp, J.E.E. van Beusekom, J. Wiktor, & J.M. Węśławski. 2006. Comparison of nematode communities in Baltic and North Sea sublittoral, permeable sands – Diversity and environmental control. *Estuarine, Coastal and Shelf Science* 70, 224–238.
- USEPA. 1999. Method 9060. Total organic carbon (TOC) in soil. EPA/SW-846, U.S. Environmental Protection Agency, Washington, DC, USA.
- USEPA. 2001. Method 200.7. Trace Elements in Water, Solids, and Biosolids by Inductively Coupled Plasma-Atomic Emission Spectrometry, Revision 5, EPA-821-R-01-010, U.S. Environmental Protection Agency, Washington, DC, USA.
- Vanaverbeke, J., K. Soetaert, C. Heip, & A. Vanreusel. 1997. The metazoan meiobenthos along the continental slope of the Globan Spur (NE Atlantic). *Journal of Sea Research* 38, 93–107.
- Vanreusel, A., et al. 2000. Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. *Deep-Sea Research I* 47, 1855–1879.
- Vincx, M., P. Meire, & C. Heip. 1990. The distribution of Nematodes communities in the southern bight of the North Sea. *Cahiers de Biologie Marine* 31, 107–129.
- Wade, T.L., Y. Soliman, S.T. Sweet, G.A. Wolff, & B.J. Presley. 2008. Trace elements and polycyclic aromatic hydrocarbons (PAHs) concentrations in deep Gulf of Mexico sediments. *Deep-Sea Research II* 55, 2585–2593.
- Wieser, W. 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. *Arkiv Zoologi* 4, 439–484.

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