

Metazoan meiofauna abundance in relation to environmental variables in the northern Gulf of Mexico deep sea

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Abstract

In order to more fully understand the distribution of meiofauna and how they respond to topographic, geochemical and physical forcing in the northern Gulf of Mexico, meiofauna abundance and environmental variables were analyzed in a hypothesis-based univariate and multivariate design. Meiofauna abundance was significantly related to water depth, but also exhibited significant longitudinal differences resulting from proximity to Mississippi River outflow. Canyon features in proximity of Mississippi River outflow were found to greatly enhance meiofauna abundance. The Florida Escarpment interacts with Mississippi River outflow and the Loop Current to enhance meiofauna abundance at stations lying directly above and below the escarpment. Multivariate comparisons of meiofauna abundance with environmental variables revealed a strong Mississippi River influence. River outflow alters local sediment characteristics, and interacts with loop current eddies and dynamic slope topography to increase particulate organic matter flux in the northeastern region, thus creating areas of higher than normal meiofauna abundance.

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1. Introduction

The first quantitative study of deep-sea meiofauna ecology was by Wigley and McIntyre (1964). Subsequent studies have been conducted in all major ocean basins; including the Atlantic, Pacific, North Sea, Mediterranean, Red Sea, Gulf of

Mexico, and Weddell Sea (see reviews by Tietjen, 1992; Soltwedel, 2000). Deep-sea investigations have focused on bathymetric gradients of abundance (Tietjen, 1971; Coull et al., 1977; Shirayama, 1984a; Aller et al., 2002; Gutzmann et al., 2004; Netto et al., 2005) and relationships of community structure with food availability (Thiel, 1978; Pfannkuche, 1993; Danovaro et al., 1995; Gooday et al., 1996; Relexans et al., 1996; Soltwedel, 1997; Fabiano and Danovaro, 1999; Sommer and Pfannkuche, 2000; Flach et al., 2002; Netto et al., 2005) and with other environmental factors (Shirayama, 1984a; Alongi and Pichon, 1988; Vanhove et al.,

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1995; Soltwedel et al., 1996). Most meiofaunal studies have focused on limited geographic areas, not allowing region- or basin-scale patterns to emerge. Therefore, deep-sea investigations of meiofauna abundance in relation to environmental factors have been limited primarily to local-scale correlations between abundance and physical or geochemical variables (Shirayama, 1984a), but have not considered large-scale regional differences in the topographic environment. Soltwedel (2000) reviewed studies in 48 regions, in each of which between 2 and 21 stations were sampled. In the majority (31) of these regions, samples were collected at less than 10 stations. Meiofauna abundance has been reported from only 15 deep-sea stations (350–2800 m) in the Northern Gulf of Mexico (Pequegnat et al., 1990) and from 16 stations (200–540 m) in the Southern Gulf of Mexico (Escobar et al., 1997). Organism distributions and how they respond to topographic, geochemical and physical oceanographic features have not been fully elucidated for any deep-sea community (Etter and Mullineaux, 2001).

The northern Gulf of Mexico continental slope is physically and geologically complex with numerous basins, knolls, and canyons. In order to more fully understand meiofaunal community structure in relation to the complex physical setting of the Northern Gulf of Mexico continental slope, meiofauna abundance was compared at 51 stations from the Florida continental slope to the Texas continental slope. The study was hypothesis-based in order to select stations covering nearly the entire northern region, taking into account the diverse physical setting. The sampling design was based on the following six null hypotheses: H_{01} —there is no difference in meiofaunal abundance with depth, H_{02} —there is no difference in meiofaunal abundance with longitude, H_{03} —there is no difference in meiofaunal abundance in versus out of submarine basins, H_{04} —there is no difference in meiofaunal abundance in versus out of submarine canyons, H_{05} —there is no difference in meiofaunal abundance with respect to escarpments, and H_{06} —there is no difference in meiofaunal abundance with respect to overlying water column primary production.

The depth hypothesis (H_{01}) follows one of the fundamental observations of deep-sea ecology: as depth increases, abundance decreases (Tietjen, 1992; Soltwedel, 2000; Aller et al., 2002; Gutzmann et al., 2004; Netto et al., 2005), presumably reflecting the

decrease in particulate organic matter (POM) flux with depth (Turley et al., 1995). The longitude hypothesis (H_{02}) was specifically designed to test for differences in meiofauna abundance along the Texas, Louisiana, and Florida margins. Mississippi River discharge is a major source of new nutrients and organic matter into the northern Gulf of Mexico, with a mean daily discharge of nearly 1 billion m^3 (<http://water.usgs.gov>). The a priori hypothesis was that a longitudinal gradient of abundance exists, which is maximized near Mississippi River outflow. The basin hypothesis (H_{03}) was designed to test for faunal differences between relatively small (5–15 km) basins and adjacent non-basin stations on the Texas/Louisiana slope. Basins, along with canyons (H_{04}), may concentrate the rain of POM and therefore enhance meiofauna abundance. Escarpments (H_{05}) may interact with deep water currents and internal waves to influence food supply, resulting in increased abundance directly below the escarpment due to enhanced sedimentation of POM (Etter and Mullineaux, 2001). Finally, increased overlying chlorophyll-*a* (chl-*a*) biomass (H_{06}) due to interactions among Mississippi River outflow, the Loop Current, and mesoscale anticyclonic/cyclonic gyre pairs all likely affect meiofauna abundance. Therefore, the purpose of this study was to integrate regional differences in complex shelf topography and environmental variables in order to more fully understand the processes controlling meiofauna abundance in the northern Gulf of Mexico deep sea.

2. Methods

2.1. Field methods

On the northern Gulf of Mexico continental slope and abyssal plain, 51 stations were sampled for meiofauna community structure (Fig. 1) as part of the Deepwater Program: Northern Gulf of Mexico Continental Slope Habitats and Benthic Ecology program (henceforth referred to as Deep Gulf of Mexico Benthos or simply DGoMB). Seven transects were investigated from 200 to 3750 m. In the northwest region, two transects (RW and W) were sampled that included 13 stations, including one station in the Alaminos Canyon (AC1). In the west-central region (WC), two historical stations from the Pequegnat et al. (1990) study were sampled in this study, but stations in this region were designed mainly to test for faunal differences

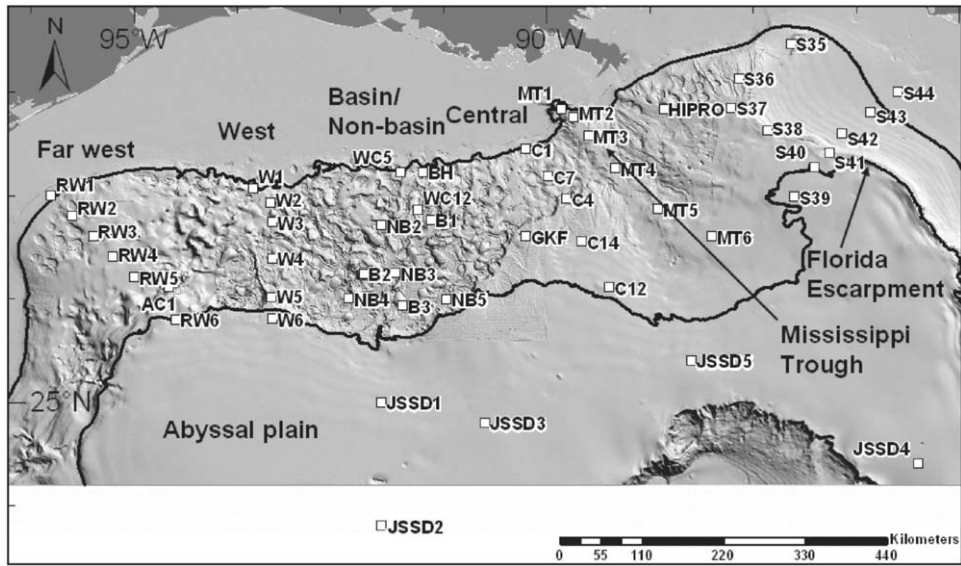


Fig. 1. Location of the 51 DGoMB stations in the northern Gulf of Mexico deep sea. Note transects and topographical features of interest (basins, canyons, Mississippi Trough, and Florida Escarpment). Highlighted contours are 300 and 3000 m. Bathymetry is courtesy of William Bryant, Texas A&M University.

between basin (B) and non-basin (NB) locations. The central transect (C) was included in the design to test for differences from the adjacent Mississippi Trough (MT) transect. In the northeast region, 10 stations from two transects were sampled perpendicular to the Florida slope and escarpment (S). Additional stations not included in the original experimental design, but added to the sampling scheme, were a highly productive station (HIPRO) in the northeastern region, a station from the Green Knoll Furrow (GKF) region, a station on Bush Hill (BH), and five stations on the Sigsbee abyssal plain as part of the Joint Studies of the Sigsbee Deep (JSSD); a collaboration with La Universidad Nacional Autónoma de México.

Survey samples were collected on a 60-day cruise aboard the R/V *Gyre* (Texas A&M University) during the months of May and June 2000. Meiofauna were collected by a 5.5 cm inner diameter (i.d.) core tube that was mounted inside the GOMEX boxcorer (Boland and Rowe, 1991). Unfortunately, the broader scope of the DGoMB project did not allow for use of a multicorer, which would have ensured higher quality quantitative samples. The subcores were mounted inside the boxcorer in order to ensure that meiofauna were collected from an undisturbed surface, thereby alleviating some of the sampling artifacts created by the boxcorer bow wave (Bett et al., 1994).

Surface disturbance can occur when the boxcorer is placed on the ship's deck. Insertion of a core tube after the boxcorer has already been brought aboard is known to create artifacts including loss of organisms. Taking the sample from an inner subcore reduces edge effects (Eckman and Thistle, 1988). The bow waves of sampling devices in deep water can have an impact on estimates of surface dwelling meiofauna (Hulings and Gray, 1971). In this study, bow wave effects were reduced by heavily weighting the boxcorer, stopping its downward motion approximately 20 m above the seafloor, and slowly lowering the corer into the sediment. One subcore sample was taken from each boxcorer sample, and five total replicates were taken from separate boxcorer casts. The top 3 cm of sediment was extruded and stored for meiofaunal community analysis. A small pilot study was conducted at station W2, and it was determined that more than 80% of total meiofauna and more than 94% of Harpacticoida are found in the top 3 cm of sediment at this station (Baguley and Montagna, unpublished data). Although meiofauna can be found down to 6 cm or deeper in Gulf of Mexico deep-sea sediments, because of the time constraints of this large study only the top 3 cm was analyzed.

After core sections were collected, meiofauna were narcotized in 7% MgCl₂ (isotonic to seawater).

Narcotizing meiofauna is necessary to minimize body shape distortion during the preservation process. Preventing animal distortion was critical for biomass calculations and taxonomic identifications (see Baguley et al., 2004; Baguley et al., 2006 in revision). Samples were then preserved in an equal volume of 10% buffered formalin (yielding a final concentration of 5% formalin) (Hulings and Gray, 1971). The buffered formalin was made up with 45 μm mesh filtered seawater to exclude plankton. Rose bengal was added to the preservative to easily distinguish meiofauna during the sorting process. Samples were then stored and returned to The University of Texas Marine Science Institute (Port Aransas, TX) for analysis.

2.2. Laboratory methods

By convention, the definition of meiofauna is those animals that pass through a 1000 μm mesh sieve but are retained on a 63 μm mesh sieve (Giere, 1993). Most deep-sea meiofaunal ecologists now use 42 μm mesh (eight of nine papers reviewed in Thistle et al., 1991) with no upper limit because deep-sea organisms are generally smaller than shallow-water organisms, but conversely, some deep-sea meiobenthic taxa are larger than functionally defined meiofaunal size limits. Therefore, to conform to other studies of deep-sea meiofauna, a 45 μm mesh sieve was used to retain meiofauna, with no upper limit (a 42 μm mesh sieve was not commercially available).

Meiofauna were extracted from sediment by the Ludox centrifugation technique (de Jonge and Bouwman, 1977). Recent quality control studies have shown that the technique extracts 95–99% of organisms over all sediment grain sizes (Burgess, 2001). Samples were then sorted to major metazoan taxonomic categories and enumerated. Meiofaunal communities are composed of two groups. Temporary meiofauna are those juveniles of the macrofauna that will eventually grow into larger organisms. Permanent meiofauna are those groups where adults are less than one mm in length, e.g., Nematoda, Copepoda, Gastrotricha, Turbellaria, Acari, Gnathostomulida, Kinorhyncha, Tardigrada, Ostracoda, and some Nemertinea, Oligochaeta, and Polychaeta. The two standard meiofauna texts (Higgins and Thiel, 1988; Giere, 1993) were used in the identification of major taxonomic groups.

A full suite of sedimentary environmental variables was analytically measured from five replicate

cores (6.7 cm i.d.), from separate boxcores, at most DGoMB stations. Sediment grain size was determined by the standard Folk settling method (Folk, 1974). Total organic and inorganic carbon were determined by standard LECO combustion techniques or by Carlo Erba elemental analyzer. Polycyclic aromatic hydrocarbons (PAHs) were measured by NOAA status and trends methods (Denoux et al., 1998; Qian et al., 1998) using gas chromatography–mass spectrometry. Trace metal analyses included atomic absorption spectroscopy, instrumental neutron activation analysis, and inductively coupled plasma–mass spectroscopy (e.g., Taylor and Presley, 1998). Geochemical variables were measured by a number of methods and instruments: O_2 , H_2S , Fe, and Mn were measured with microelectrodes (Brendel and Luther, 1995; Luther et al., 1998); total CO_2 was measured via gas chromatography; sulfate was measured via ion chromatography; pH was measured with electrodes; nutrients (nitrate, nitrite, ammonia, urea, phosphate, and silicate) were measured by standard autoanalyzer techniques; dissolved organic carbon (DOC) was measured by a high-temperature combustion DOC analyzer; and organic carbon and nitrogen were measured by a Carlo Erba elemental analyzer. Surface seawater chl-*a* was estimated from Sea viewing Wide-Field Sensor (SeaWiFS) satellite imagery. The complete environmental variable data set is not presented here, but will be publicly accessible from the Geochemical & Environmental Research Group (<http://www.gerg.tamu.edu>) with appropriate permission.

2.3. Univariate statistical analysis

Six main hypotheses were investigated for differences in meiofauna abundance. For statistical power, five replicate samples were taken per station, from five separate box cores. Five transects, RW, W, C, MT and S, were included in the depth/longitude (H_{01}/H_{02}) analysis ranging from the Texas slope in the west to the Florida Escarpment in the east (Fig. 1, Table 1). Five stations were included per transect, over five depth zones, consistent between transects. The test for differences between basin and non-basin (H_{03}) locations included three B and three NB stations (Fig. 1, Table 1). The sampling design blocked basin and non-basin stations (B1 with NB2, B2 with NB3, and B3 with NB4), to control for differing distances from shore. The test for differences in meiofauna abundance

Table 1

Summary of meiofauna community structure experimental design: null hypotheses, design criteria, and stations included in analysis

Null hypotheses	Design criteria	Stations included	No. stations
H ₀₁ and H ₀₂ Depth and longitude	Five replicate transects spanning the entire northern GOM continental slope, over five depths	MT1, 3–6 RW1–2, 4–6, AC1 C1, 4, 7, 12, 14 W1, 3–6 S35–37, 39, 44	25
H ₀₃ Basin/non-basin	Three basin stations, three non-basin stations, over three distances from shore	B1–3 NB2–4	6
H ₀₄ Canyon/non-canyon	Two replicate transects over five depths	MT1, 3–6 C1, 4, 7, 12, 14	10
H ₀₅ Escarpment/non-escarpment	Two replicate transects over six distances from shore	S39–44 W1–6	12

See Fig. 1 and related text for complete description of station locations, hypotheses, and experimental design.

between canyon and non-canyon (H₀₄) locations included stations from the MT and adjacent C transect (Fig. 1, Table 1). Five MT stations were paired with five C stations at five common depth zones, thus removing the effect of depth. The effect of escarpments (H₀₅) on meiofaunal abundance was tested by comparing an escarpment transect to a non-escarpment transect (Fig. 1, Table 1). Six stations per transect were paired at approximately equal distance from shore and distances between stations.

Differences in meiofaunal abundance, with respect to H₀₁–H₀₅, were tested using a two-way completely random analysis of variance (ANOVA). Prior to analysis, abundance was $\log_{10}(N+1)$ transformed to meet assumptions of the general linear model, and Shapiro–Wilks W and Levene's tests were employed using the SAS UNIVARIATE procedure to test for normality and homogeneity of variance, respectively.

Differences in meiofaunal abundance due to overlying water column primary production (H₀₆) were tested by comparing surface water primary production estimates to meiofauna abundance at 43 stations. Mean biweekly chl-*a* data (SeaWiFS satellite imagery), for the 2 months prior to community structure sampling (March–April 2000), were included in a log-linear regression and multivariate comparison (see below) of biotic and abiotic variables. Averaging for 2 months prior to sampling was done to remove short-term temporal variation.

2.4. Multivariate statistical analysis

Both parametric (sensu Montagna and Harper, 1996) and non-parametric (sensu Warwick and Clarke, 1991) statistical analyses were implemented. Biotic variables were analyzed primarily by non-parametric procedures, which included multidimensional scaling (MDS) and analysis of similarity (ANOSIM) of meiofauna abundance data. Abiotic environmental variables were analyzed by parametric principal components analysis (PCA). PCA is a procedure to reduce a large set of intercorrelated variables into a smaller set of orthogonal (completely uncorrelated) variables. Each new variable (principal component) accounts for a percentage of the total variance in the original data set. The new variables are extracted in decreasing order of variance, such that the first few principal components (PCs) explain most of the variation in the data set. The contribution of each environmental variable to the new PC is called a load. Typically, the new PC loads can be interpreted to indicate structure in the data set. Each observation contributing to the PC is called a score. Thus, the main advantage of PCA is the generation of station scores, which are interpretable, and can subsequently be used in other analyses (i.e. correlation or regression with abundance).

Environmental variables included in the environmental PCA included chl-*a* in the overlying water column as measured from SeaWiFS satellite images. Chl-*a* was adjusted for remineralization with

increasing water depth by application of the exponential model proposed by Betzer et al. (1984) and updated by Berger et al. (1988). The amount of surface chl-*a* reaching the sea floor is described by the equation

$$J(z) = 0.409PP^{1.41} / Z^{0.628}$$

where $J(z)$ is the flux of chl-*a* transported downwards through some depth Z and PP is the overlying water column chl-*a* concentration. The remaining variables were all from sediments and included grain size (sand, silt, and clay content), total PAHs excluding perylene, the trace metals calcium (Ca), chromium (Cr), tin (Sn), and strontium (Sr), total organic nitrogen (OrgN), particulate organic carbon (POC), DOC, ammonium (NH_4^+), urea, and nitrate (NO_3^-).

Prior to analysis, all data were transformed to validate assumptions of parametric tests and to weight the contribution of high or low measurements. The angular transformation ($x = \arcsin \sqrt{|y|}$) was used for the sediment grain-size data, and a natural logarithm transformation ($x = \log_e[|y + 1|]$) was used on all other data.

One common problem with environmental data is that many variables measuring the same effects can skew the result. Thus, pre-analysis was performed to determine if certain classes of variables could be dropped from the analysis. Only the total PAHs were used because it served as a proxy for all organic contaminants. A total of 29 metals were measured and had to be reduced for the final analysis using an initial PCA of metals only. The first metals principal component (PC1) accounted for 70.1% of the total variance in the metals data set, and was the only PC with an eigenvalue greater than one. Thus, four metals, the two with highest positive and negative loadings, were chosen for the final PCA analysis. These four metals (listed above) served as a proxy for the general trace metal pattern seen at all stations.

ANOVA and PCA procedures were conducted using SAS statistical software (SAS Institute Inc., 1989). Non-parametric MDS as well as rarefaction calculations (ES) were conducted in Primer 5.0 (Clarke and Warwick, 2001). Geographic information systems (GIS)-based analyses were performed (ArcView 9.0, ESRI) to further examine spatial trends in the data set. The relative abundance at each station was compared by generating bubble values, where bubble size (the circle size at each

station location) is relative to total meiofauna abundance at each station.

3. Results

3.1. General results

A total of 586 samples from 51 stations (Table 2) in the study yielded 1.71×10^5 individuals from 21 meiofauna taxa. Mean abundance (extrapolated to $\text{N } 10 \text{ cm}^{-2}$) per station was $2.63 \times 10^3 \text{ N } 10 \text{ cm}^{-2}$ with a standard deviation of 2.01×10^3 . Maximum and minimum meiofauna abundances were found at stations MT1 and JSSD3 with values of 9.46×10^3 and $0.60 \times 10^3 \text{ N } 10 \text{ cm}^{-2}$. A strong linear relationship existed between log abundance ($R^2 = 0.658$, $P < 0.0001$) and water depth (Fig. 2). Spatial analysis in meiofauna abundance (bubble size representing relative abundance) reveals highest values in the shallow northeastern stations (Fig. 3). Relatively lower abundance was observed in the western transects, but the general trend of decreasing abundance with depth was consistent along western transects (RW and W) and in the west-central area (WC5, WC12, B1-B3, NB2-NB5). Exceptionally high abundance was found at stations MT1, MT3, S35, S36, S42 and C7, all located in the northeast region at depths ranging from approximately 450 to 1900 m. Departure from the general pattern of decreasing abundance with depth was observed at these northeastern stations.

The meiofauna community was composed of individuals from 21 taxonomic groups (Table 3). Nematoda and Harpacticoida (including nauplii) were the two dominant groups accounting for 65.3% and 25.4% of individuals, respectively. Unknown fauna were the next most abundant, comprising 6.6% of individuals. The unknown group likely included representatives from various soft-bodied taxa including (but not limited to) various taxa within the Turbellaria and representatives of the Protista (e.g., Ciliophora). Soft-bodied taxa, such as these, often become unrecognizable during bulk fixation with buffered formaldehyde. The remaining 3.7% of the meiofauna community was composed of various taxa, including Polychaeta, Kinorhyncha, Ostracoda, Cyclopoida, Tardigrada, Tanaidacea, Nemertinea, Acari, Isopoda, Bivalvia, Gastrotricha, Anthozoa, Priapulida, Gastropoda, Aplacophora, Rotifera, Sipuncula, and Loricifera (Table 3). The complete major taxa data set is not presented here, but will be publicly

Table 2
Location and depth of each DGoMB station and the average meiofaunal abundance ($N\ 10\text{ cm}^{-2}$) from five replicate cores

Station	Latitude	Longitude	Depth (m)	Abundance ($N\ 10\text{ cm}^{-2}$)
AC1	26.39357	-94.57308	2440	1300
B1	27.20254	-91.40522	2253	1574
B2	26.55001	-92.21508	2635	1399
B3	26.16445	-91.73510	2600	1558
BH	27.78000	-91.50000	545	4079
C1	28.05984	-90.24992	336	3691
C12	26.37973	-89.24030	2924	1388
C14	26.93824	-89.57251	2495	1466
C4	27.45315	-89.76308	1463	2736
C7	27.73044	-89.98203	1066	5421
GKF	27.00000	-90.25000	2460	843
HIPRO	28.55000	-88.58000	1565	3431
JSSD1	25.00000	-92.00000	3545	875
JSSD2	23.50000	-92.00000	3725	873
JSSD3	24.75000	-90.75000	3635	604
JSSD4	24.25000	-85.50000	3400	635
JSSD5	25.50000	-88.25000	3350	1357
MT1	28.54111	-89.82502	482	9457
MT2	28.44793	-89.67195	677	5352
MT3	28.22151	-89.49405	990	8860
MT4	27.82761	-89.16615	1401	2461
MT5	27.33284	-88.65607	2267	1290
MT6	27.00165	-87.99913	2743	1553
NB2	27.13483	-92.00007	1530	1683
NB3	26.55803	-91.82255	1875	1652
NB4	26.24675	-92.39229	2020	1484
NB5	26.24540	-91.20991	2065	1173
RW1	27.50014	-96.00285	212	4118
RW2	27.25403	-95.74681	950	2195
RW3	27.00836	-95.49236	1340	2488
RW4	26.75142	-95.25018	1575	2328
RW5	26.50753	-94.99672	1620	1706
RW6	25.99730	-94.49558	3000	1445
S35	29.33515	-87.04636	668	5016
S36	28.91851	-87.67215	1826	8000
S37	28.55363	-87.76685	2387	2912
S38	28.27995	-87.32759	2627	1572
S39	27.48368	-86.99982	3000	832
S40	27.83948	-86.75142	2972	995
S41	28.01364	-86.57335	2974	1814
S42	28.25100	-86.41927	763	4925
S43	28.50294	-86.07679	362	2763
S44	28.74999	-85.74770	212	3185
W1	27.57717	-93.55101	420	3872
W2	27.41393	-93.34033	625	2633
W3	27.17240	-93.32329	875	2626
W4	26.73082	-93.31973	1460	1878
W5	26.26777	-93.33272	2750	1046
W6	26.00285	-93.32028	3150	1242
WC12	27.32324	-91.55581	1175	2184
WC5	27.77591	-91.76568	348	4121

Latitude and longitude are expressed as decimal degrees. Negative longitudinal values denote the western hemisphere.

accessible from the Texas A&M University Geochemical and Environmental Research Group (<http://www.gerg.tamu.edu/>) with appropriate permission.

3.2. Univariate analysis

The Shapiro–Wilks W test indicated that log-transformed meiofauna abundance was normally distributed ($P = 0.4303$); likewise, Levene's test indicated homogeneity of variance ($P = 0.2104$). In the test for differences over depth and longitude (H_{01} and H_{02}), significant main effects for longitude and depth were observed ($P < 0.0001$, Table 4). However, a significant longitude by depth interaction term ($P < 0.0001$, Table 4) was also observed. The two western transects (RW and W) had a gradual linear decrease in abundance with depth (Fig. 3). With increasing proximity to the Mississippi River, (transects C and MT) abundance increased greatly at stations between 300 and 1000 m, i.e., C1, C7, and MT1-3 (Fig. 3). The Florida slope transect (S) had highest abundance at station S36 (ca. 2000 m), which was located in the DeSoto Canyon. Abundance over all transects became more similar at all stations deeper than 2500 m water depth (Fig. 3).

In the test for differences between basin and adjacent non-basin stations (H_{03}), no significant difference was observed between main effects ($P = 0.5421$, and 0.7773 , Table 4), and no significant interaction was observed ($P = 0.6980$, Table 4).

In the test for differences between canyon and adjacent non-canyon stations (H_{04}), significant treatment ($P = 0.0059$) and depth zone ($P < 0.0001$) effects were observed (Table 4), but a significant interaction term was also observed ($P = 0.0058$, Table 4). Abundance was elevated at the head of the canyon (MT1 and MT3) compared to stations of similar depth in the adjacent transect (C1 and C7) (Fig. 3). However, the two transects became increasingly similar with depth and revealed no differences at stations greater than 1500 m, i.e., C14, C12, and MT4-6 (Fig. 3).

In the test for differences in meiofauna abundance due to the presence of an escarpment (H_{05}), no significant escarpment effect was observed in comparison to the reference transect ($P = 0.791$). However, a significant main effect was observed for distance from shore ($P < 0.0001$, Table 4), and a significant interaction term was observed ($P = 0.002$, Table 4). Abundance was dramatically

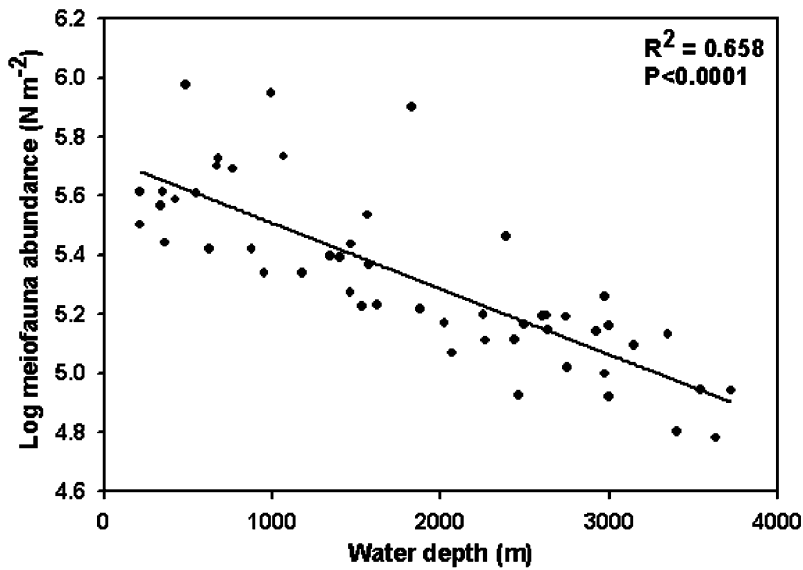


Fig. 2. Log₁₀(x + 1) transformed meiofauna abundance (N 10 cm⁻²) versus water depth (m) for all stations sampled during DGoMB project. Abundance decreases in a strong log-linear relationship.

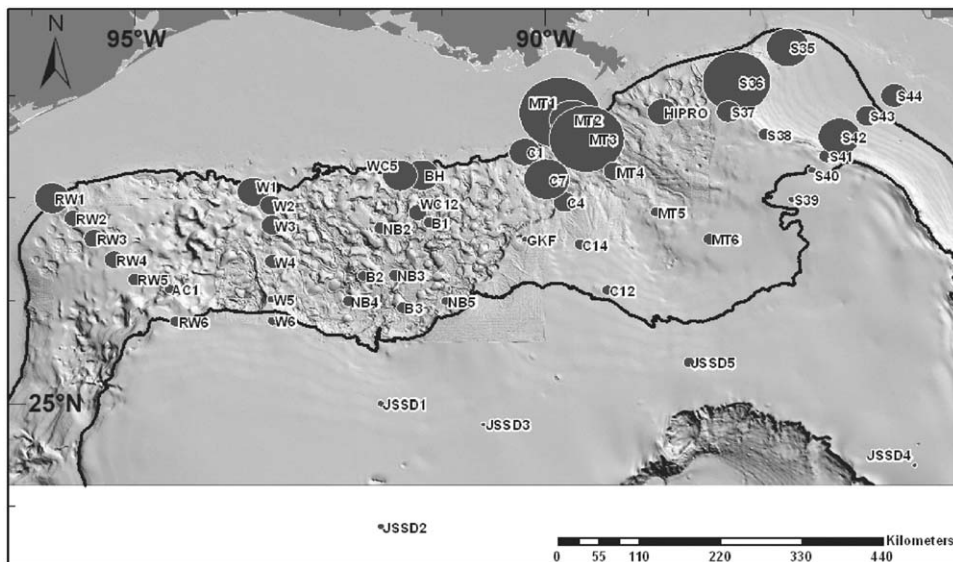


Fig. 3. Spatial analysis of meiofaunal abundance (N 10 cm⁻²) at all DGoMB stations. Buffer size equals relative meiofauna abundance. Bathymetric and longitudinal patterns of abundance are apparent. Note high mid-depth abundance in the northeastern region (stations MT3, S36, C7, and S42). The highlighted contours are at 300 and 3000 m water depth. Bathymetry is courtesy of William Bryant, Texas A&M University.

lower below the Florida Escarpment than above (Fig. 3). Station S41 had nearly twice the abundance of stations S40 and S39, which are of similar depth but further offshore. Comparison to the reference transect in the western gulf (stations W1–W6) illustrates deviation of the escarpment transect from

an expected decrease in abundance along a relatively constant slope, with elevated abundance just above and below the escarpment (Fig. 3).

The amount of overlying water column chl-*a* biomass that reaches the sea floor decreased in a log–log relationship with depth (Fig. 4A), that is

Table 3

Average abundance (AA) ($N\ 10\ cm^{-2}$), percent contribution (Contrib.%) to the total abundance, and cumulative percent contribution (T%)

Taxa	AA ($N\ 10\ cm^{-2}$)	Contrib.%	T%
Nematoda	1747	65.3	65.3
Nauplii	315	13.1	78.4
Harpacticoida	311	12.3	90.7
Unknown	157	6.6	97.3
Polychaeta	53	1.5	98.8
Kinorhyncha	11	0.3	99.1
Ostracoda	11	0.3	99.5
Cyclopoida	9	0.2	99.6
Tardigrada	4	0.1	99.8
Tanaidacea	3	0.1	99.9
Nemertinea	3	0.1	99.9
Acari	1	0.0	100.0
Isopoda	1	0.0	100.0
Bivalvia	1	0.0	100.0
Gastrotricha	0	0.0	100.0
Anthozoa	0	0.0	100.0
Priapulida	0	0.0	100.0
Gastropoda	0	0.0	100.0
Aplacophora	0	0.0	100.0
Rotifera	0	0.0	100.0
Sipuncula	0	0.0	100.0
Loricifera	0	0.0	100.0

T% = Contrib.% of each group plus the Contrib.% of each previous group. Data summarized for all 51 stations (average of five replicate 5.5 cm i.d. cores per station).

described by the inverse first-order equation: $y = y_0 + a/x$, ($R^2 = 0.518$). Meiofauna abundance increased with increasing overlying water column chl-*a* biomass (Fig. 4B). Although the linear regression fits the data reasonably well ($R^2 = 0.413$, $P < 0.0001$), the data more closely followed the exponential power function $y = ax^b$ ($R^2 = 0.619$); but considerable variance exists in the relationship. Although null hypothesis six (H_{06}) was not tested with ANOVA as above, detailed analysis of the meiofauna community with respect to food availability and sediment environmental variables was accomplished with multivariate procedures (see below).

3.3. Principal components analysis

In the PCA, the first three principal components accounted for 61.5% of the total variance in the data set (Table 5). However, four PCs out of 15 had eigenvalues greater than one, which means that the first four were significant. The sign of variable loads (negative or positive) indicates gradients in concen-

Table 4

ANOVA results, tests for differences in meiofauna abundance

Source	DF	SS	MS	F	P
H₀₁ and H₀₂—Depth/longitude					
Long.	4	1.222	0.305	12.07	<.0001
Depth	4	5.867	1.467	57.94	<.0001
Long. × Depth	16	3.104	0.194	7.67	<.0001
Error	100	2.531	0.025		
H₀₃—Basins					
Basin	1	0.012	0.012	0.38	0.5421
DFS	2	0.016	0.008	0.25	0.7773
Basin × DFS	2	0.023	0.011	0.37	0.6980
Error	56	1.708	0.031		
H₀₄—Canyons					
Canyon	1	0.167	0.167	8.58	0.0059
Depth	4	3.931	0.982	50.41	<.0001
Canyon × Depth	4	0.338	0.085	4.34	0.0058
Error	36	0.702	0.019		
H₀₅—Escarpment					
Escarp.	1	0.001	0.001	0.07	0.7906
DFS	5	2.998	0.600	50.51	<.0001
Escarp. × DFS	5	0.279	0.056	4.70	0.0015
Error	46	0.546	0.012		

Dependent variable = $\log_{10}(N+1)$. ANOVA abbreviations: DF = degrees of freedom, SS = sum of squares, MS = mean square, F = F-test value, P = $Pr > F$. Factor abbreviations: long. = longitude, basin = basin vs. non-basin stations, dfs = distance from shore, escarp. = escarpment vs. non-escarpment transects.

trations. Variables that load negatively will have highest concentrations for negative PC loads with decreasing concentrations moving in the positive direction, and vice versa. PC1 accounted for 33.5% of the total variance, had high positive loadings by clay, total PAHs, Sn, Cr, and had high negative loadings by sand, Sr and Ca (Table 6, Fig. 5A). PC1 is interpreted as the sediment properties, with high silt, clay, organic (PAH) and metal (Cr and Sn) contaminants near the Mississippi River, and higher sand and natural background metals (Ca and Sr) with increasing distance from the Mississippi River.

PC2 accounted for 16.7% of the total variance and had highly positive loadings by chl-*a* and POC, weak positive loadings by OrgN and NH_4^+ , and weak negative loadings by NO_3^- and urea (Table 6, Fig. 5A). PC2 is interpreted as POM flux. PC3 accounted for 11.3% of the total variance and had highly positive loadings by DOC and highly negative loadings by urea (Table 6, Fig. 5B). PC4 accounted for 10.2% of the total variance and had moderate positive loadings by silt, NH_4^+ , NO_3^- , and

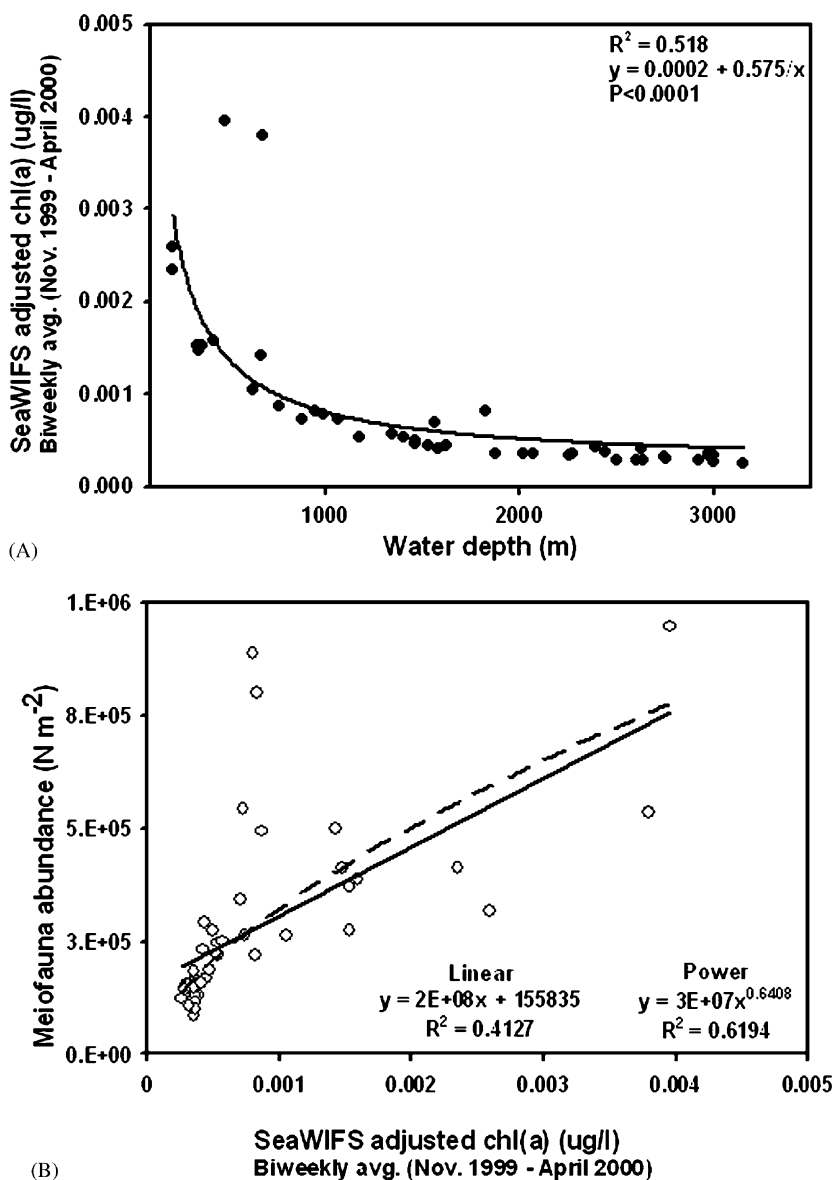


Fig. 4. SeaWiFS chl-*a* ($\mu\text{g/L}$) biweekly average (November 1999 through April 2000). Chl-*a* concentration was adjusted for remineralization with depth (see Berger et al., 1988). (A) Inverse first-order relationship of adjusted chl-*a* with water depth. Chl-*a* concentration decreases with depth reflecting rapid remineralization in surface waters. (B) Meiofauna abundance versus adjusted chl-*a*. Despite considerable heterogeneity in primary production in northern Gulf of Mexico surface waters; however, a relationship with benthic meiofauna abundance exists.

PAH (Table 6). However, PC3 and PC4 did not have obvious interpretations. PCs 1–4 were regressed against abundance to determine if they were significantly related to the biotic community. PC1 had a weak, but significant, positive relationship with meiofauna abundance, but accounted for only 22% of the variance in the biotic data set (Fig. 6A, $R^2 = 0.215$). PC2 had a moderate, and significant, relationship with meiofauna abundance (Fig. 6B,

$R^2 = 0.303$). PC3 and PC4 did not have significant relationships with abundance.

3.4. Multidimensional scaling

MDS analysis of major taxa abundance data revealed a strong trend with depth (Fig. 7). Depth zones of 1000 m depth increments grouped together with only moderate overlap. Two groups can be

Table 5

Eigenvalues of the correlation matrix for the environmental PCA, proportion of variance explained by each principal component, and cumulative variance

PC	Eigenvalue	Difference	Proportion	Cumulative
1	5.019	2.504	0.335	0.335
2	2.515	0.818	0.168	0.502
3	1.697	0.162	0.113	0.615
4	1.535	0.606	0.102	0.718
5	0.929	0.077	0.062	0.780
6	0.851	0.217	0.057	0.837
7	0.635	0.044	0.042	0.879
8	0.591	0.060	0.039	0.918
9	0.530	0.218	0.035	0.954
10	0.312	0.111	0.021	0.974
11	0.201	0.066	0.013	0.988
12	0.135	0.105	0.009	0.997
13	0.030	0.017	0.002	0.999
14	0.014	0.008	0.001	1.000
15	0.005	0.000	1.000	1.000

Table 6

Variable loads for the rotated (varimax) factor pattern of the environmental PCA. See text for variable descriptions

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Chl- <i>a</i>	0.11096	0.90356	-0.00047	0.08619	0.03993
Sand	-0.76437	0.21025	0.20489	-0.19623	-0.48221
Silt	0.43118	-0.03573	0.05246	0.65701	0.25268
Clay	0.65541	-0.28278	-0.27347	-0.09372	0.52084
NH ₄	-0.26511	0.35890	0.18627	0.66324	0.12841
POC	-0.04478	0.81893	0.06908	0.05581	0.08796
UREA	0.01605	-0.14464	-0.80871	-0.09793	0.09566
NO ₃	-0.19939	-0.49356	-0.21657	0.53803	-0.07637
DOC	-0.09904	-0.03622	0.87375	-0.00081	-0.06273
OrgN	-0.00531	0.27374	-0.10288	0.11126	0.88406
TPAHWP	0.55797	0.14311	0.14306	0.55440	-0.19339
Ca	-0.87212	-0.30214	0.09420	-0.23840	0.02223
Sr	-0.85733	-0.25022	0.14018	-0.20549	0.05741
Cr	0.86572	-0.12582	-0.06502	-0.16531	0.09411
Sn	0.83863	-0.00196	0.14965	-0.17825	-0.01304

defined, one representing stations less than 2000 m and a second group greater than 2000 m (Fig. 7). These two groups are statistically different by ANOSIM ($P < 0.01$). The depth trend is a reflection of decreasing abundance of the dominant taxonomic groups, for example, Nematoda (Fig. 8), where the bubble value is proportional to nematode abundance. Decrease in meiofauna abundance with depth was, we believe, largely a result of POC concentration, which is apparent when bubble

values proportionate to variable concentration are overlaid (Fig. 9). POC concentration also follows the MDS depth trend and reflects decreasing food supply and therefore, abundance, with increasing water depth.

4. Discussion

4.1. Abundance in relation to bathymetry, longitude, and topographic features

Meiofauna abundance was significantly correlated with water depth (Fig. 2, Table 4), a trend that has been observed worldwide (Tietjen, 1992; Soltwedel, 2000; Aller et al., 2002; Gutzmann et al., 2004; Netto et al., 2005). Depth-related trends are attributed to a decreasing supply of organic matter with increasing depth and distance from land (Thiel, 1978; Pfannkuche, 1993; Danovaro et al., 1995; Gooday et al., 1996; Relexans et al., 1996; Soltwedel, 1997; Fabiano and Danovaro, 1999; Shimanaga and Shirayama, 2000; Gooday, 2002). This general pattern was observed in the northern Gulf of Mexico (Figs. 2 and 3) but some variability existed that may be attributed to physical and geological complexity of the continental slope and interactions with overlying water column processes. Between-transect variation in meiofauna abundance occurs at shallow to mid-depth stations (200–2000 m) (Figs. 2 and 3). Therefore, the pattern of decreasing abundance with depth is dependent upon differences in near-shore input of POM.

A significant longitude by depth interaction ($P < 0.0001$, Table 4) indicates that meiofauna abundance changed differently with depth, depending on proximity to Mississippi River outflow (Fig. 3), corroborating observations of a recent study in the northeast Atlantic (Flach et al., 2002). Maximum abundance values were observed in the Mississippi Trough (Fig. 3). Mississippi River outflow brings nutrients that drive overlying primary production but also carries terrigenous organic matter, further fueling benthic secondary production (Meybeck, 1993). Highest meiofauna abundance values within the Mississippi Trough also corresponded with a significant canyon effect ($P = 0.006$), compared to the adjacent C transect (Table 4). Although not included in the statistical analysis for canyon effects, station S36, which lies in the DeSoto Canyon, also has unusually high abundance, further evidence that canyon features support higher meiofaunal standing stocks (Fig. 3).

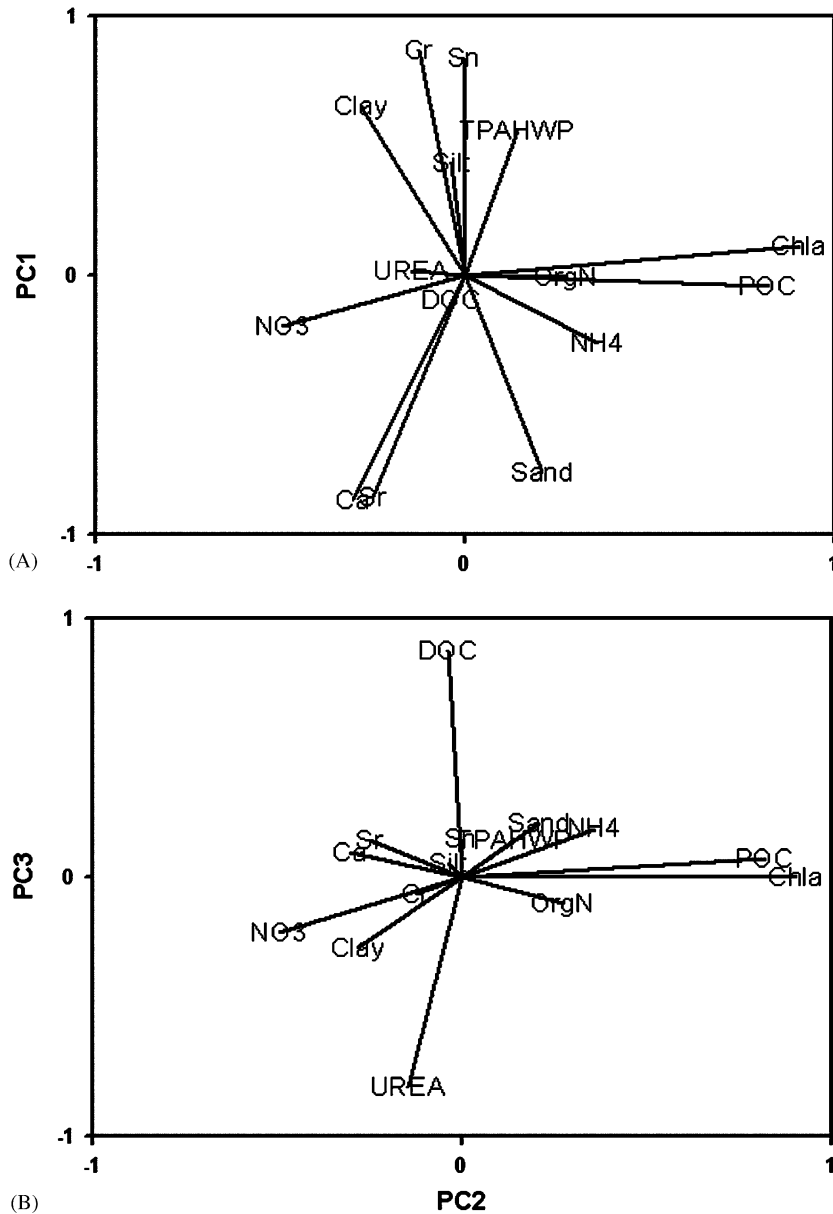


Fig. 5. Principal components analysis of environmental variables. (A) Variable loading scores for PC1 versus PC2. (B) Variable loading scores for PC2 versus PC3. Variables are as follows: Chl-*a* = chlorophyll-*a*, sand, silt, clay, NH₄ = ammonium, POC = particulate organic carbon, urea, NO₃ = nitrate, DOC = dissolved organic carbon, OrgN = total organic nitrogen, TPAHWP = total polycyclic organic hydrocarbons without perylene, Ca = calcium, Sr = strontium, Cr = chromium, Sn = tin.

On the contrary, basin features do not support higher meiofauna abundance compared with adjacent non-basin areas ($P = 0.542$). This suggests that POM does not preferentially accumulate in the basins studied, compared to the adjacent non-basin slope.

The effect of the Florida Escarpment on meiofauna abundance, in comparison to a reference

transect, had a highly significant interaction with distance from shore. The significant interaction indicates that meiofauna abundance responded differently to precipitous depth increases, compared to gradual depth increases. Spatial analysis using GIS (Fig. 3) and comparison to the reference transect in the western Gulf indicate abundance “hot spots” directly above (S42) and below (S41)

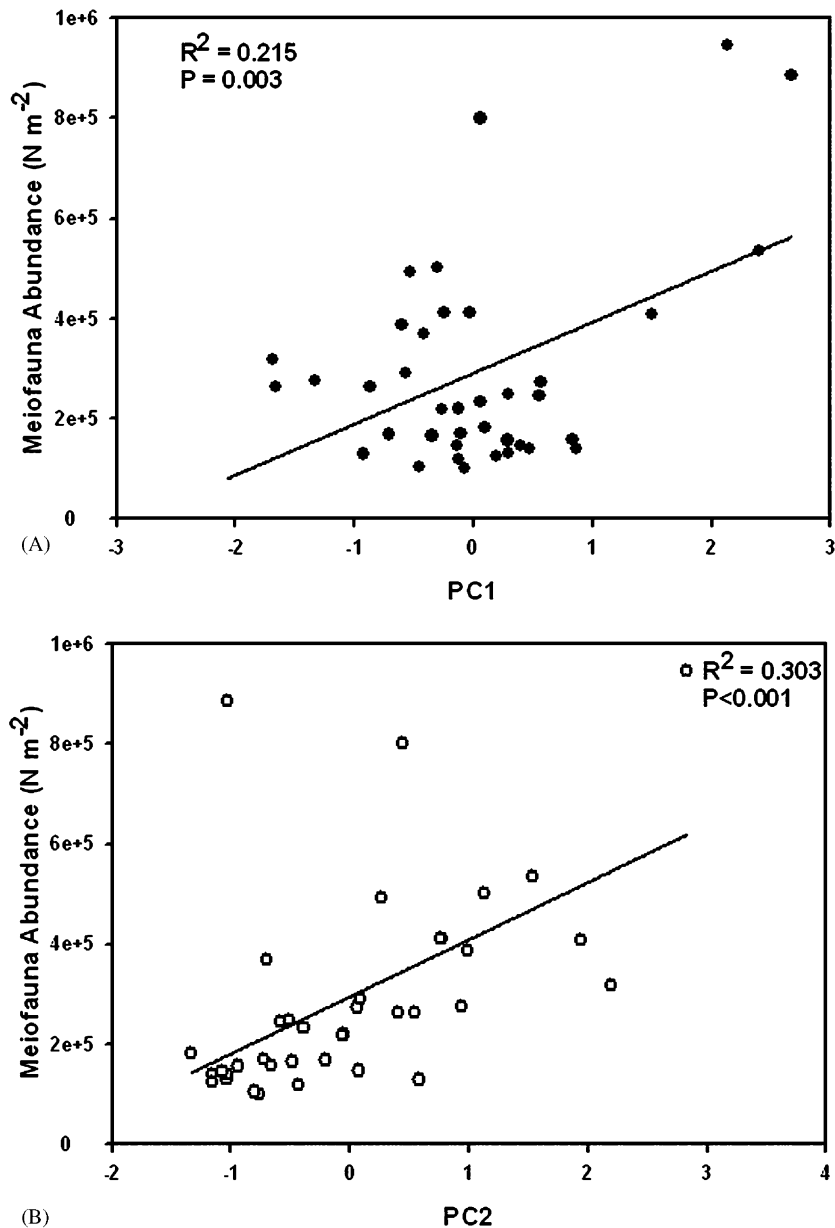


Fig. 6. (A) Meiofauna abundance ($N m^{-2}$) regressed against environmental PC1, (sediment properties). (B) Meiofauna abundance ($N m^{-2}$) regressed against environmental PC2 (POM Flux). Although variance from the regression is high in both cases, the relationships are significant ($P = 0.003$ and $P < 0.001$, respectively).

the escarpment, confirming the a priori hypothesis. Sedimentation rates at station S42 were 4–5 times greater than those observed at stations MT3 and S42 (Yeager et al., 2004). The mean path of the Loop Current results in current impingement on the escarpment, which likely results in advection of nutrients and organic material from Mississippi River inflow and additionally could create upwel-

ling or downwelling zones along the escarpment, depending on the depth of the current. Upwelling would bring new nutrients to the surface and enhance surface primary production; conversely, downwelling could facilitate advected surface primary and secondary production to the benthos. Meiofauna abundance at station S42 is two-fold greater than at stations S43 and S44. Meiofauna

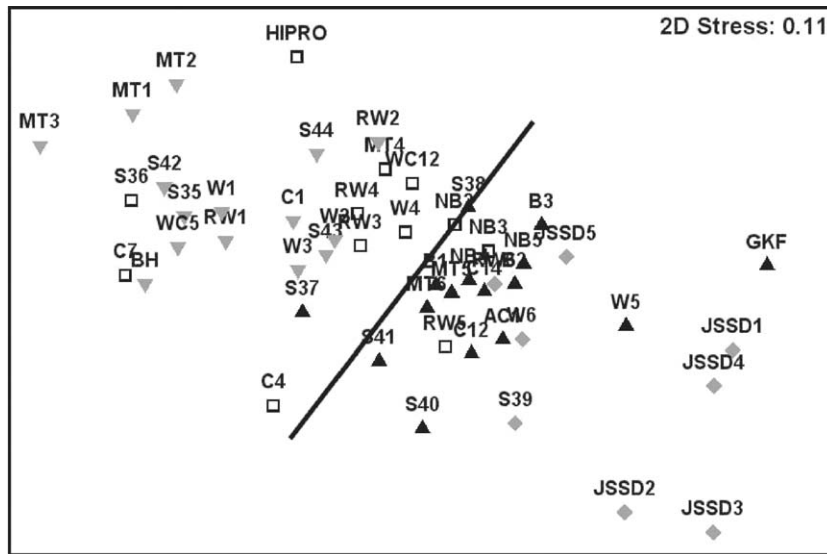


Fig. 7. MDS ordination of DGoMB stations, based on Bray–Curtis similarity (4th root transformation) of major taxa abundance. Symbols indicate depth zones of 1000-m increments: ▼ = 200–1000 m, ■ = 1000–2000 m, ▲ = 2000–3000 m, and ◆ ≥ 3000 m. Solid line represents the approximate break between stations above and below 2000 m.

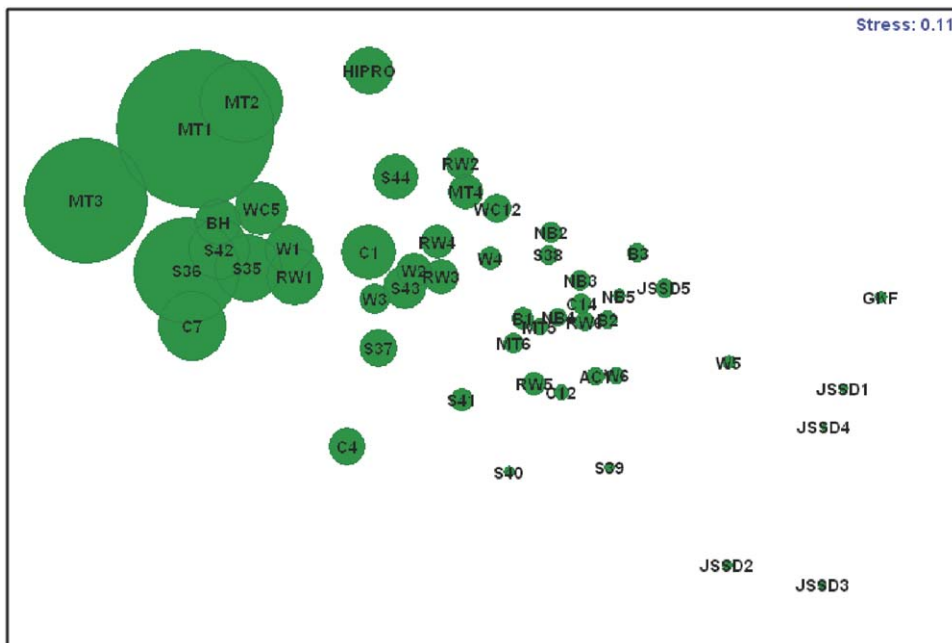


Fig. 8. MDS ordination of DGoMB stations, based on Bray–Curtis similarity (4th root transformation) of major taxa abundance. Bubble size equals relative nematode abundance at each station. The MDS plot strongly represents decreasing abundance with depth.

abundance was greatly enhanced in the vicinity of the escarpment compared to the relatively constant Texas/Louisiana slope (Fig. 3); this may be partially attributed to changes in sediment grain size, but is more likely a result of increased POM flux in this region.

4.2. Relationship with biological, biogeochemical, and geological variables

Meiofauna abundance was compared to surface water chl-*a* biomass estimates by SeaWiFS satellite imagery, adjusted for remineralization with depth

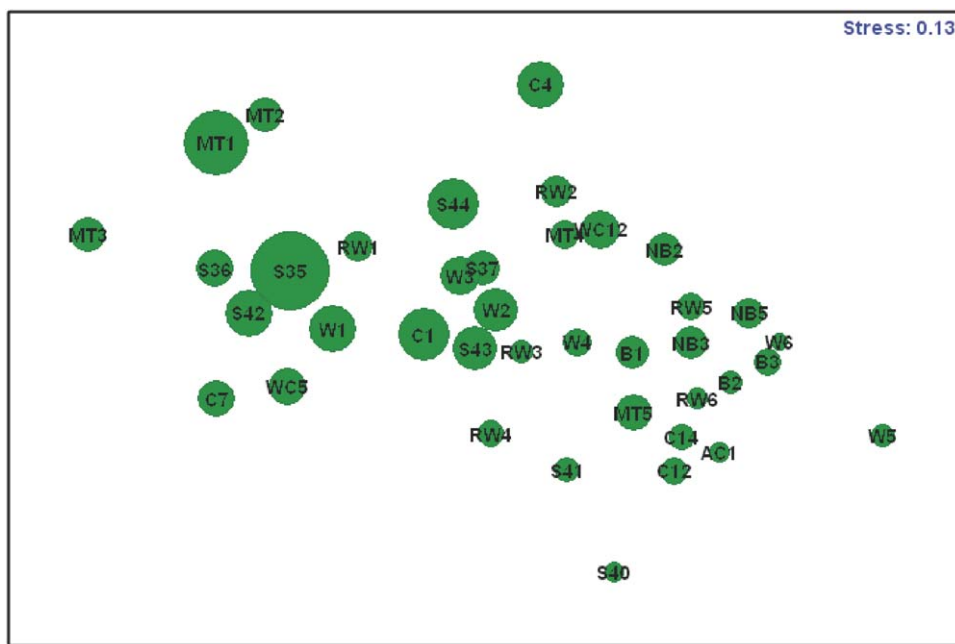


Fig. 9. MDS ordination of DGoMB stations, based on Bray–Curtis similarity (4th root transformation) of major taxa abundance. Bubble size equals relative particulate organic carbon (POC) concentration, which generally decreases with increasing depth. *Note*: JSSD stations omitted from this plot due to lack of environmental data at those locations.

(Berger et al., 1988) (Fig. 4A). Meiofauna abundance had a significant relationship with adjusted chl-*a* biomass (Fig. 4B). It is not surprising that highest chl-*a* biomass is observed in the vicinity of the Mississippi Trough, corresponding to highest meiofauna abundance. Estimates of chl-*a* biomass by satellite imagery should be interpreted with caution. SeaWiFS accuracy is quite high and acceptable for blue water environments with little or no river plume influence (Hu et al., 2003). On the contrary, stations with high river plume influence tend to be overestimated because of the presence of particulate inorganic and organic matter in terrestrial runoff. All DGoMB stations were in blue water, lending confidence to our estimates. Interactions between Loop Current eddies and Mississippi River outflow, which result in offshore advection of turbid shelf water (Hu et al., 2003), is the likely source of high chl-*a* biomass in this region.

The multivariate analysis of environmental variables adequately described the offshore environment in the northern Gulf of Mexico. The 51 stations differed moderately with respect to geochemistry, trace metal concentration, grain size, and organic contaminants (Figs. 5A and B), depending on their proximity to Mississippi River outflow. Regression of meiofauna abundance against enviro-

mental PC1 (sediment properties) indicated that this component accounted for 22% of the variance in the meiofauna standing stock (Fig. 6A). Differences in sediment grain size and heterogeneity have been previously shown to influence meiofauna abundance (Gerlach, 1977; Coull et al., 1982; Netto et al., 2005), with a trend toward increasing meiofauna abundance in silt dominated sediments, as observed here for stations with positive PC1 scores (Fig. 6A). Sediment porosity greatly affects vertical meiofauna distribution, with deeper dwelling organisms in sandy or calcareous ooze environments compared to clay-dominated sediments (Shirayama, 1984b). Although a few northern Gulf of Mexico stations had highly sandy sediments (S43, S44, W2, W3, and MT5), most stations had little sand and higher concentrations of silt and clay. Stations near Mississippi River outflow had high silt and also had highest meiofauna abundance (Figs. 5A, 6A). Meiofauna and other benthic organisms are known to concentrate in surface sediments (Thiel, 1972; Coull et al., 1977; Dinét and Vivier, 1977; Vivier, 1978; Shirayama, 1984b), a fact that has been attributed to food and oxygen availabilities (Ansari et al., 1980; Shirayama, 1984b) resulting from differing sediment regimes. This idea is corroborated here.

Meiofauna abundance was more strongly related to environmental PC2 (POM flux), which accounted for 30% of the variance in meiofaunal abundance (Fig. 6B). Meiofauna are known to respond to organic matter input (Thiel, 1978; Pfannkuche, 1993; Danovaro et al., 1995; Gooday et al., 1996; Relexans et al., 1996; Soltwedel, 1997; Fabiano and Danovaro, 1999; Gutzmann et al., 2004; Vanaverbeke et al., 2004), and this study provides new insight into physical–biological interactions taking place over larger spatial scales that affect the flux of organic matter to the deep-sea floor. Furthermore, the environmental PCA adequately described the geochemical and geological state of northern Gulf of Mexico sediments and the relationship with meiofaunal community abundance.

4.3. Synthesis

Spatial analysis of meiofaunal abundance (Fig. 3) across the entire northern Gulf of Mexico reveals a strong difference between northwestern and northeastern stations, which was confirmed by a significant depth by longitude interaction (Table 4). The central offshore Gulf of Mexico is also characterized by a somewhat typical pattern of seasonal primary production, with winter chl-*a* maxima (December–February) and summer chl-*a* minima (Müller-Karger et al., 1991). By comparison, the northeastern Gulf of Mexico has high biweekly variations in surface chl-*a* biomass, even throughout summer months (Hu et al., 2003). Differences in surface water chl-*a* biomass between northwestern and northeastern regions of the Gulf of Mexico are attributed to an interaction between two factors: (1) the presence of the Loop Current and (2) Mississippi River outflow to the western GOM, which averages $1 \text{ billion m}^3 \text{ d}^{-1}$ (<http://water.usgs.gov>).

Loop Current eddies impinge onto the continental slope and shelf in the northeastern Gulf of Mexico, resulting in lateral transport of low salinity/high chl-*a* waters from the shelf over the slope (Qian et al., 2003). Offshore transport of shelf waters over the slope can influence underlying benthic communities by stimulating greater primary production, by lateral input of terrigenous organic matter, or by lateral input of organic matter produced over the shelf. Loop Current eddies were regularly observed in the northeastern Gulf of Mexico in the months prior to and during community structure sampling, as visible from TOPEX/Poseidon sea surface

altimetry (data generated by CCAR: <http://e450.colorado.edu/realtime/welcome/>).

Canyon and escarpment features in the northeastern Gulf of Mexico also interact to enhance meiofaunal abundance (Table 4, Fig. 3). Large topographical features likely interact to create flows that alter food supply (Gage and Tyler, 1991; Etter and Mullineaux, 2001; Yeager et al., 2004) and therefore increase abundance (Thistle et al., 1985, 1991). High shallow and mid-depth abundance in the Mississippi Trough and DeSoto Canyon, respectively, suggest canyon features have a concentrating effect on POM flux. Loop Current or Loop Current eddy impingement on the Florida Escarpment (Schmitz, 2004) creates a high-energy hydrodynamic environment as observed by ship-board ADCP (Acoustic Doppler Current Profiler) current profiles during sampling cruises (Rowe et al., in prep). Therefore, it is not surprising that meiofauna abundance was greatly enhanced directly above and below the Florida Escarpment (Fig. 3).

Meiofauna abundance in the northern Gulf of Mexico deep sea is regulated by interactions between sediment characteristics and POM flux, which are related to Mississippi River outflow, circulation processes, and the complex topographic nature of the continental slope. Meiofauna abundance is significantly related to water depth but also exhibits significant longitudinal differences resulting from proximity to Mississippi River outflow. Canyon features in proximity of Mississippi River outflow were found to greatly enhance meiofauna abundance. The Florida Escarpment interacts with Mississippi River outflow and the Loop Current to enhance meiofauna abundance at stations lying directly above and below the escarpment. Multivariate comparisons of meiofauna abundance with environmental variables reveal a strong Mississippi River influence. River outflow alters local sediment characteristics and interacts with loop current eddies and dynamic slope topography to increase POM flux in the northeastern region, thus creating meiofauna abundance hot spots. In contrast, northwestern Gulf of Mexico stations exhibited a typical bathymetric pattern of decreasing abundance with depth, and basin features west of Mississippi River influence did not support enhanced abundance. Therefore, the meiofauna community in the northern Gulf of Mexico deep sea is regulated by complex spatial interactions between Mississippi River outflow, physical oceanographic processes, and the physical complexity of the

continental slope, which regulate the supply of POM to the sea floor.

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