Complex depth-related patterns in taxonomic and functional diversity of polychaetes in the Gulf of Mexico

Russell Carvalho [a,*], Chih-Lin Wei [b], Gilbert Rowe [a,c], Anja Schulze [a,c]

[a] Department of Oceanography, Texas A&M University, College Station, TX 77843, USA
[b] Ocean Science Centre, Memorial University of Newfoundland, St. John's, Canada NL A1C 5S7
[c] Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553, USA

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ABSTRACT

Patterns of taxonomic and functional diversity in polychaete assemblages were examined in the deep northern Gulf of Mexico, including the first analysis of polychaete feeding guild distribution. An analysis of samples from a total of 51 stations located along 7 transects plus additional nearby sites, indicated that density decreased exponentially with depth, with the central locations having higher densities than the eastern and western regions. Alpha diversity was also highest at the central stations associated with the Mississippi trough. The samples can be grouped into three significant clusters based on thirty percent similarity of species composition. BIO-ENV indicated depth, sediment particle size, and export POC were most important variables explaining distributions. The diversity of polychaete feeding guilds was high in the Mississippi trough, upper and mid-slope regions but declined to a few guilds on the Sigsbee abyssal plain. Combining feeding guild analysis with traditional analysis of species diversity contributes to a clearer understanding of trophic diversity in deep-sea benthic assemblages.

1. Introduction

Observing broad-scale patterns of macrobenthic biodiversity is an important aspect of many deep-sea studies. The 'classic' phenomenon of a parabolic curve with a mid-depth maximum (MDM) of species diversity has been reported in numerous deep-sea studies. Cosson-Sarradin et al. (1998) studied total macrofauna in the northeast Atlantic and observed a parabolic trend in the diversity of polychaetes, representatives of a dominant taxon in that region. Deep-sea species diversity typically peaks at mid-slope depths between 2000 m and 3000 m for regions of the western North Atlantic (Rex, 1983; Rex et al., 1993). Similar parabolic patterns of diversity were observed during a series of intense deep-sea sampling programs in the Atlantic (Paterson and Lambshead, 1995; Flach and de Bruin, 1999; Gage et al., 2000), as well as the Eastern Pacific and Indian Oceans (Levin and Gage, 1998). Pequegnat et al. (1990) focused on patterns of macrofaunal diversity in the Gulf of Mexico (GoM) and observed uniformly high polychaete species diversity (55 species per station) up to a depth of 1465 m, with a subsequent decrease (22 species per station) at 3000 m. Their results revealed a decrease in macrofaunal diversity

from the east to the west, with the absence of a parabolic diversity trend. They concluded that diversity patterns are primarily the result of seasonal and regional variations. Pérez-Mendoza et al. (2003) sampled 10 stations along a bathymetric gradient (200–3760 m) in the Sigsbee basin and reported an atypical inverted parabolic curve for abyssal polychaetes in the GoM. These results suggest that the unique hydrodynamics and the geomorphology of the GoM play an important role in shaping the observed patterns in species diversity.

Riverine input into the GoM is extensive. It includes 20 major river systems (> 150 rivers) along the coast of the United States, Mexico and Cuba (Moody, 1967). The Mississippi discharges on an average 21,700 m^3 per second of fresh water into the Gulf, with an average nitrogen influx of 1,470,000 and total phosphorus influx of 140,000 metric tons (Aulenbach et al., 2007). This nutrient loading from the Mississippi has caused an increase of inorganic N and P for the past 50 years, resulting in high productivity (Rabalais et al., 2002) that may directly or indirectly influence the diversity and functioning of benthic communities, especially in the deep sea (Snelgrove et al., 1992).

Haedrich et al. (2008) mapped species richness for various taxa in the GoM using a generalized linear model (GLM). Polychaete richness was highly correlated to food, suggesting that the observed patterns were primarily due to levels of productivity in the GoM. The quality, quantity and the timing of organic input to the deep-sea benthos are key factors that influence the benthic

* Corresponding author. Tel.: +1 409 4546417.
E-mail addresses: russell_carvalho@yahoo.com,
russell64@tamu.edu (R. Carvalho).

polychaete community structure (Cosson et al., 1997; Shields and Hughes, 2009). Using sea-surface chlorophyll (SSC) data, Biggs et al. (2008) estimated export POC (particulate organic carbon) flux at 49 sampling sites of the Deep Gulf of Mexico Benthos program (DGoMB). They suggested that cross-margin flows generated by mesoscale eddies move low salinity high-chlorophyll Mississippi water offshore, ultimately leading to a higher POC input to the benthos in the Northeast GoM. Similarly, Wei et al. (2010a) reported food availability as a controlling factor for macrofaunal depth zonation in the GoM. Morse and Beazley (2008) highlighted strong correlations between organic carbon contents in the deep-water sediments and the abundance and biomass of macrofauna and meiofauna. These studies warrant a comprehensive examination of the role of food input in shaping the patterns of polychaete diversity in the GoM.

Polychaetes play a significant role in ecosystem function (Pagliosa, 2005; Bremner, 2008; Wagner and Barros, 2011). Dominant in terms of both abundance and species number, this taxon is widely used to assess community patterns and species richness estimates of macrofaunal benthic assemblages (Olsgard and Somerfield, 2000). Their diverse functional traits provide clues to ecological processes in deep-sea benthic environments and can be used for deciphering species diversity patterns (Pagliosa, 2005; Pacheco et al., 2011). The feeding guild concept of Fauchald and Jumars (1979) classified polychaetes into trophic groups based on morphology and their inferred feeding behavior. This pioneering effort was followed by a series of studies that utilized feeding guilds, most recently to investigate the reoxygenation and colonization potential of deep-burrowing polychaetes (Granberg et al., 2008), to interpret assemblage patterns (Domínguez-Castanedo et al., 2012; Wagner and Barros, 2011), to assess environmental conditions (Pagliosa, 2005), and to study the impacts of seafloor hydrodynamics on benthic fauna (Dolbeth et al., 2009). A traditional Linnean classification system may not always be adequate for describing the biodiversity, health and functioning of the deep marine realm (Warwick and Somerfield, 2008). Instead, taxon-specific functional traits are more useful in providing vital clues to ecosystem function (Woodin, 1987; Aarnio et al., 2011; Wagner and Barros, 2011) as well as modeling the flow of energy and

matter through benthic systems (Christensen and Pauly, 1993; Pacheco et al., 2011).

Our aims in this study were (1) to re-assess large-scale trends in the composition and density of deep-sea benthic polychaete communities on the northern continental slope of the GoM, and (2) to test potential factors responsible for the observed patterns of distribution and their occurrence. We hypothesize that depth-related trends in feeding guild diversity are distinct from those in taxonomic diversity. Additionally, we predict that the magnitude of food input is the most important factor in shaping the taxonomic and functional diversity of deep-sea organisms.

2. Materials and methods

2.1. Study site

Extensive sampling of the sea floor in the deep waters of the Northern GoM was carried out between 2000 and 2002 during three cruises of the Deep Gulf of Mexico Benthos Program (DGoMB). Surveying a broad region of the northern Gulf, this study examined the community structure and function of the biota of the GoM. Stations sampled ranged from 22°–30°N latitude to 85°E–96°W longitude at a depth range of 200–3700 m (Fig. 1; Table S1).

2.2. Sampling methods

Samples were collected from 51 stations on the R/V *Gyre*. Macrofaunal specimens were collected using a 0.2-m^2 version GOMEX boxcore (Boland and Rowe, 1991). The boxcore collected at least 5 replicate cores per station. Sediment from the top 15 cm (covering an area of 1.725 m^2) was sieved at 300-μm mesh size, fixed in 10% seawater-buffered formalin and stored in 70% ethanol for permanent preservation. Polychaete feeding guilds were classified according to Fauchald and Jumars (1979). Only those samples that could be identified to species level (in some cases tentatively) were included in our analyses. The feeding guilds are a three-letter code, the first letter indicating the major feeding mode
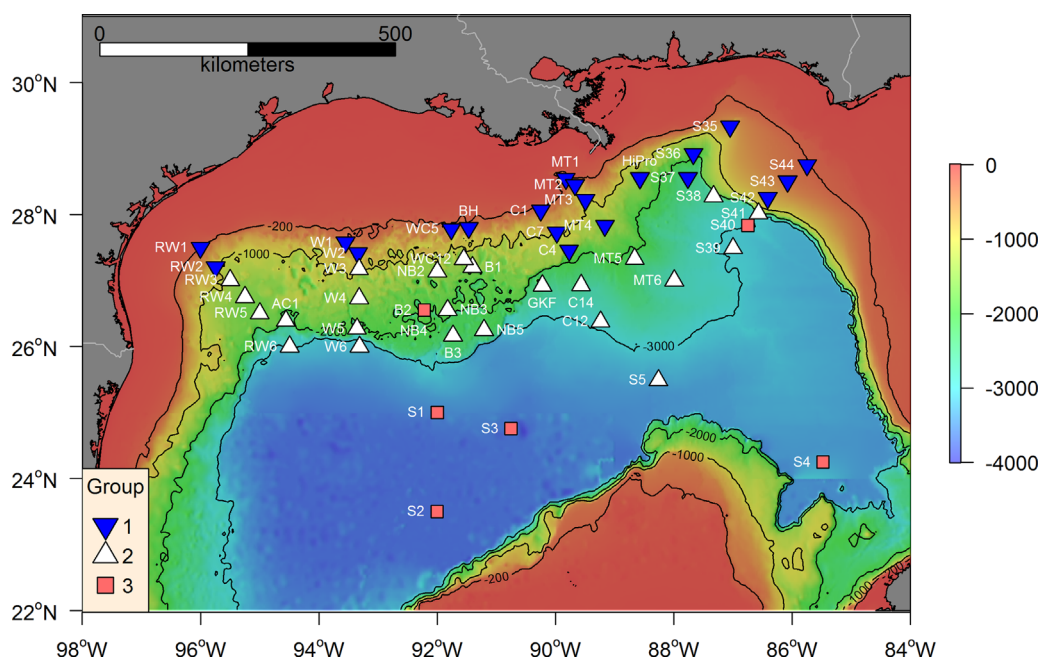

Fig. 1. Sampling stations for DGoMB cruises in the Gulf of Mexico. Symbols indicate significant faunal group ($p < 0.01$).

where S, surface deposit-feeder; B, subsurface deposit-feeder; C, carnivore; F, filter-feeder; O, omnivore; and H, herbivore. The second letter indicates the motility designated as M, motile; D, discretely motile; and S, sessile. The third letter indicates the major morphological structure used in feeding that show P, pumping; J, jawed; T, tentaculate; X, other structures like unarmed proboscides; and S, eversible pharynges, which are sac-like feeding structures.

2.3. Data analysis

Polychaete samples were sorted and separated to their lowest taxonomic unit. Volumetric dimensions of specimens were measured from selected stations (MT1, S42, MT3, C7, S36 and MT6, Fig. 1) for 3 sub-cores within a boxcore using an ocular micrometer (Nunnally, 2003). These biovolumes were converted to wet weight assuming macrofaunal density of 1.13 mg mm^{-1} (Gerlach et al., 1985), and then to carbon weight based on a taxa-specific conversion factor for polychaetes (5.1%; Rowe, 1983).

Species abundance (species-by-site) and guild abundance (guild-by-site) matrix was 4th-root transformed and the pairwise similarities between sites were calculated using the Bray–Curtis index (Bray and Curtis, 1957). Utilizing group average clustering, the Bray–Curtis similarities among locations were presented as a dendrogram (Clarke and Gorley, 2006). A similarity

profile test (SIMPROF) was performed to ensure that the faunal zones were comprised of significant branches ($p < 0.01$). The Bray–Curtis similarities based on species abundance as well as guild abundance were visualized by the non-metric Multi-Dimensional Scaling (MDS).

Biological diversity is composed of two important properties: evenness and richness (Magurran, 2004). We used Pielou's equitability index (J') to measure the evenness component of the community diversity (species) and functional diversity (feeding guilds). To measure richness, we used the rarefaction index (Hurlbert, 1971) to compute the expected number of species $E(S_n)$ and expected number of feeding guilds $E(G_n)$ from 50 randomly selected individuals. The $E(S_n)$ or $E(G_n)$ is a robust method for numerically comparing the community and functional diversity with a standardized sample size (numbers of individuals in a sample). Average similarity within groups and the dissimilarity between groups were broken down to similarity percentage (SIMPER) contribution to determine how individual species contributed to faunal zonation. The individual species contributions were pooled by the feeding guild types to examine guild contribution across different faunal zones. Analysis of Similarity (ANOSIM) was used to test differences in species composition as well as guild composition among sampling locations.

A total of 15 environmental variables, including depth (m), potential temperature (°C), salinity (psu), sigma-theta (kg m^{-3}),
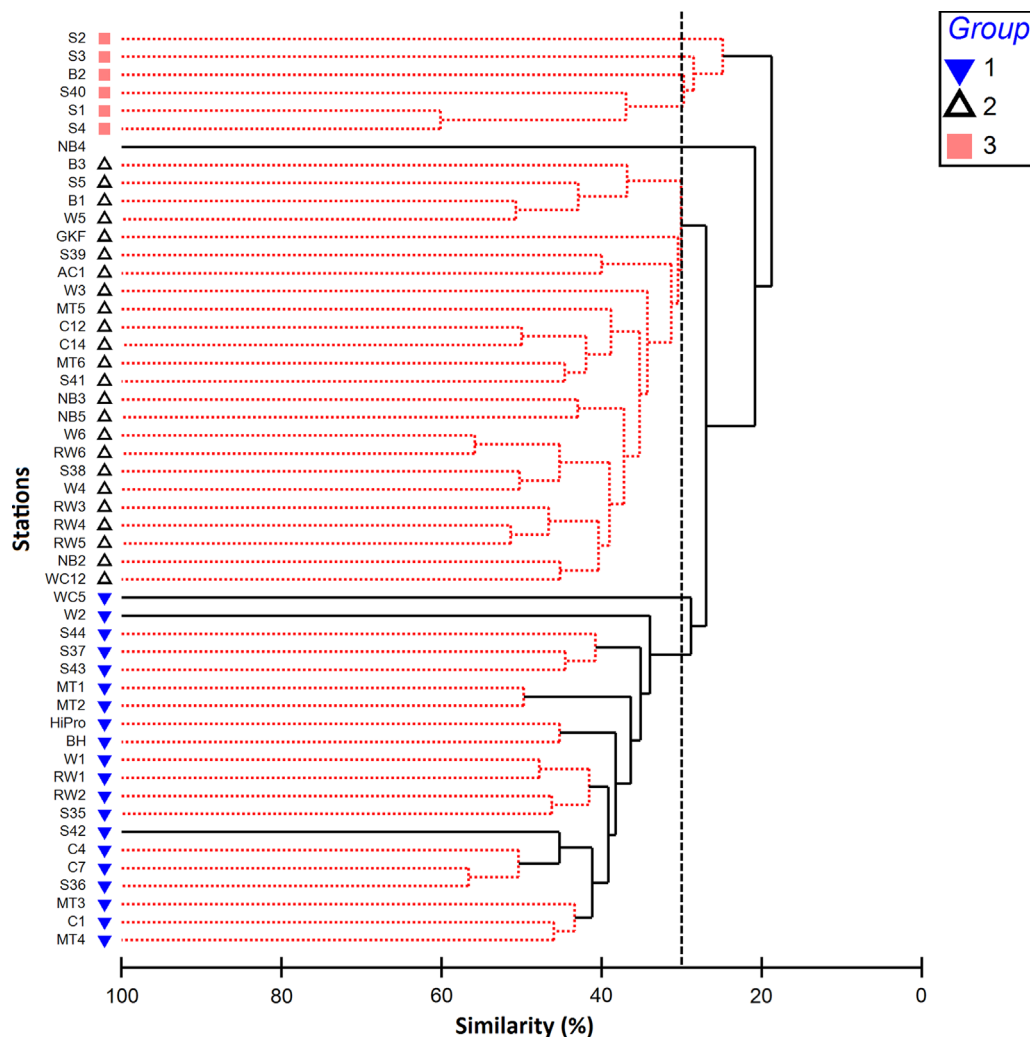

Fig. 2. Cluster analysis based on 4th-root transformed site-by-species abundance and Bray–Curtis similarity for DGoMB stations. Solid lines indicate significant branches (SIMPROF, $p < 0.01$). DGoMB station numbers are listed on the left and each statistically significant group (at 30% level) is assigned a different symbol. The x-axis indicates Bray–Curtis similarity.

relative fluorescence (volts), oxygen (ml L^{-1}), PO$_4$ (micromoles L^{-1}), NO$_3$ (micromoles L^{-1}), SIO$_3$ (micromoles L^{-1}), particulate matter (PM), Sand (%), Silt (%), Clay (%), export particulate organic carbon (POC) flux (mg C m^{-2} day^{-1}), and total polynuclear aromatic hydrocarbons (PAH's) with perylene (TPAHWP) (mg g^{-1}), were measured along with the biological samples. All variables were log (x+1) transformed before subjecting them to a principal component analysis (PCA). The PCA fitted orthogonal principal axes to the multivariate environmental data. The majority of the environmental variance is explained by the first 2 principal axes, with the relative variance explained corresponding to their "Eigenvalues". The principal axis is a linear combination of the environmental variables. The coefficients of the linear equation (or Eigenvectors) show the strength and direction of increasing environmental values (as arrows on the PCA plot). To see the influence of environmental factors on polychaete assemblage structure, the observed polychaete groupings were superimposed on the PCA ordination. Clear separation of polychaete grouping on the PCA plot suggests strong environmental influence on assemblage structure. Moreover, the BIO-ENV procedure was employed to choose the subsets of environmental variables 'best' correlating with faunal similarities.

Univariate and multivariate analyses were conducted using the software package SPSS$^{©}$, PRIMER v6 and PERMANOVA+ (Clarke and Gorley, 2006). The graphics and GIS mapping used R Statistical Computing Environment (R Core Team, 2012). The complete dataset and lists of variables are located in the archives of the US Department of the Interior, Bureau of Ocean Environmental Management (BOEM) and in the Ocean Biogeographic Information System (OBIS).

3. Results

3.1. Multivariate analysis of polychaete species data

Hierarchical cluster analysis with SIMPROF identified three significant clusters ($p < 0.01$) on the basis of percent similarity (< 30%) among stations (Fig. 2). Group 1 comprised a majority of the upper-slope sites (∼200–1000 m) with an extension to the

mid slope (∼1000–2000 m) in the Northeast GoM (Fig. 1). Group 2 occupied the mid to lower slope (∼1000–3000 m) of the Northwest GoM but comprised the lower slope and deep Mississippi Sediment Fan (∼2000–3300 m) sites in the Northeast GoM. Group 3 consisted of a majority of sites from the abyssal plain region ($p < 0.01$). Groups 2 and 3 showed a simple structure with no significant branching within groups. However, Group 1 is split into 5 subgroups with 40% similarity: (1) the eastern mid slope consisting of C1, C4, C7, MT3, MT4, S36 and S42; (2) western upper slope and the head of the De Soto Canyon: W1, RW1, RW2 and S35; (3) Bush Hill and High productivity sites: BH and HiPro; (4) upper Mississippi Canyon: MT1 and MT2; and (5) eastern upper slope and lower slope of De Soto Canyon: S43, S44, S37 (Table 1). A single station NB4 formed a group by itself on the basis of percent similarity (< 30%) and most likely represents an outlier.

The MDS plot on species abundance data (Fig. 3a, stress=0.19) confirmed results from cluster analysis (Fig. 2) and revealed 3 main groupings at 30% similarity. The same faunal groupings can be clearly identified by the MDS that was conducted on the guild abundance data (Fig. 3b, stress=0.15). We standardized the guild abundance by total abundance and thereafter computed Spearman's rank correlations with x and y axes of the MDS plot. The correlation coefficients were used as coordinates to plot arrows to show the direction of increasing proportion of specific guild types. The angles between arrows indicate correlations between the feeding guilds in terms of their relative abundance. For example, the proportion of SMT increased toward the Group 3 or increased with depth (Fig. 3b), whereas SST, SDJ, SDT and ODJ increased in proportion towards Group 1 or toward shallower depths (Fig. 1). SIMPER revealed which species contributed the most to the differences seen in the entire sampling region as well as individual faunal groups (Table S2 under supplemental information).

3.2. Dominant taxa and functional groups of polychaete species in the Gulf of Mexico

Approximately 17,881 specimens, representing 532 species of polychaetes, were identified. The species were assigned to a total

Table 1
List of stations grouped on the basis of percent similarity of species composition.

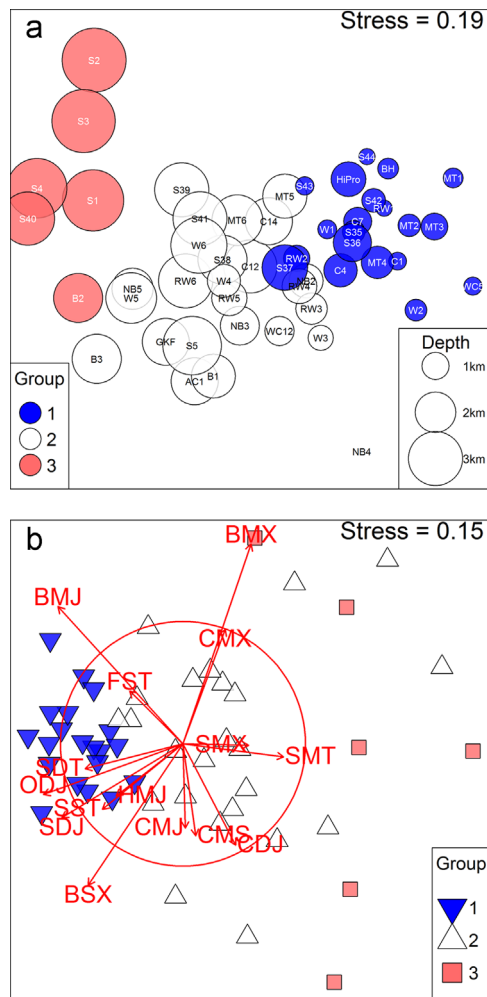| Description of area	Group no.	Station	Depth (m)	Description of area	Group no.	Station	Depth (m)
Eastern mid-slope	1	WC5	400	Mixed area	2	C14	2487
		C4	1455			AC1	2501
		C7	1080			GKF	2452
		S36	1925			NB2	1530
		S42	767			RW3	1320
		S43	366			RW2	950
		S44	215			S37	2388
		C1	334			RW4	1570
		MT3	983			W3	860
		MT4	1401			S41	2974
		NB4	2030			NB3	1875
Western Upper-slope/Desoto canyon head	1	RW1	213			NB5	2070
		W1	379			RW5	1620
		W2	625			RW6	3015
		S35	658			W6	3140
Bush hill and high productivity site	1	BH	546			S38	2635
		HiPro	1572			W4	1420
Upper Mississippi canyon	1	MT1	482			S39	3007
		MT2	676			WC12	1168
Mixed area	2	B3	2650	Abyssal plain	3	B2	2630
		B1	2260			S1	3528
		W5	2755			S2	3732
		S5	3312			S3	3675
		MT5	2275			S4	3410
		MT6	2750			S40	2975
		C12	2922				

Fig. 3. (a) nMDS ordination analysis based on 4th-root transformed site-by-species abundance and Bray-Curtis similarity. Bubbles size indicates the sample depth and color indicates significant faunal groups. (b) nMDS ordination analysis of 4th-root transformed site-by-guild abundance and Bray-Curtis similarity. The arrows indicate Spearman's rank correlation coefficients of relative abundance of each guild with MDS1 and MDS2 axis. The large circle indicates that the sum of squared correlation coefficient equals 0.5.

of 16 possible feeding guild types. Overall, the number of feeding guilds declined sharply with depth. Feeding guilds that made the largest contribution at all sampled stations were SMX (23.4%), SDT (17%), BMX (16%), SMT (10.4%) and CMJ (8%) based on SIMPER contribution percentages (Fig. 4a). The SIMPER analysis of the three groups obtained from the cluster and nMDS analyses identified the species that contributed most to the differences between these groups above a 30% similarity level. Table S2 under supplemental information displays the average abundance originally 4th-root transformed (no scale) for each species, the average Bray–Curtis similarity for each group as well as each species, the ratio of average contribution in terms of similarity divided by the standard deviation (Sim/SD) across all samples and lastly the contribution, as well as cumulative percentage, for each species. For example, the average Bray–Curtis similarity for Group 1 was 32.6% where 27 species contributed towards 90.7% of the total similarity.

The Group 1 stations were dominated by the non-selective deposit feeder *Levinsenia uncinata* and the surface deposit feeders *Aricidea suecica*, *Tharyx marioni* and *Spiophanes berkeleyorum*. Accordingly, the feeding guilds SMX (21%), SDT (17.7%), BMX (13%), CMJ (12.8%) and HMJ (6.3%) made up the majority of the percentage contribution of species for this group (Fig. 4b). Group

2 was dominated by surface deposit feeders *Paraonella monilaris* and *Aricidea suecica* and the subsurface deposit feeder *Tachytrypane* sp A. The feeding guilds SMX (26.4%), BMX (17%), SDT (16.5%) and SMT (11.2%) made up the majority of the percent contribution of species for this group (Fig. 4c). The western upper slope area occupied by this group (Table 1) was dominated by carnivorous syllid polychaetes *Sphaersyllis piriferopsis*, *S. glandulata* and *S. aciculata*. The eastern mid-slope areas were dominated by the surface deposit feeders *A. suecica*, *A. simplex*, *T. marioni*, and the carnivorous polychaetes *Paramphinome* sp. A *and Protomystides bidentata*. Lastly, Group 3 was chiefly dominated by the polychaetes *P. monilaris*, *Macrochaeta clavicornis* and *Sigambra tentaculata*. The deposit-feeders *Sabidius coronatus*, *Fauveliopsis* sp. A, *T. marioni*; and the carnivorous polychaetes *Synelmis klatti* and *Sigambra tentaculate* were other important polychaetes for this region. The most prevalent feeding guilds SMX, SDT, BMX and SMT made up 27.5%, 21.5%, 19.7% and 13.4% of the total percent contribution respectively (Fig. 4d).

Average dissimilarities observed between the three groups were generated using the SIMPER function in PRIMER v6™ (Table 2). Species showing high-percentage contributions to the average dissimilarity among groups were also found to be abundant at other stations sampled. For example, fewer species of *P. monilaris* contributed to some of the highest dissimilarity observed between Group 2 and Group 3, although it was abundant in Group 1. A high dissimilarity distance value for *P. monilaris* was an indication of a low similarity observed within groups defined by PRIMER as a cluster. The highest levels of dissimilarity among the three groups stood out as statistically different from the rest of the groups (SIMPROF, $p < 0.01$, Table 2). A one-way ANOSIM on feeding guild site-by-species abundance confirmed statistical differences across all groups (ANOSIM, $R = 0.464$, $p < 0.001$). Values generated for 'R' were used to measure the extent of group separation between 0 and 1.

3.3. Polychaete density and biomass

Mean polychaete density showed a significant exponential decline with increasing depth (Fig. 5a). The total abundance of polychaete species for all stations sampled during the DGoMB program are shown in the supplementary Table S3. The central regions were higher compared to the eastern and western areas, which were most likely influenced by their close proximity to the axis of the Mississippi Canyon. Some of the highest polychaete densities were also observed at individual stations closer to the mouth of Mississippi River along the upper slope and the mid-slope areas (Table 3). The lowest mean density was at station S4 on the Sigsbee Abyssal Plain.

In selected sites (MT1, S42, MT3, C7, S36 and MT6; Fig. 1), mean polychaete body size also showed a significant exponential decline with depth (Fig. 5b). The mean size varied from 32.7 ± 10.1 (S.E.) to 134.3 ± 76.1 (S.E.) µg carbon on the upper slope (C7 and S42, respectively) and 2.5 to 4.8 µg carbon on the lower and mid slope (MT6 and S36, respectively). The overall mean size was 62.9 ± 20.4 (S.E.) µg of carbon. The size measurements were heavily skewed toward the lower values; hence, the y-axis of Fig. 5b is shown in natural log scale.

Polychaete biomass was estimated in two ways. First, the biomass was estimated by multiplying mean density (Fig. 5a) with the overall mean body size (62.9 µg carbon). The biomass estimation and fitted line are shown as open symbols and dashed line in Fig. 5c. Second, depth-dependent body sizes were calculated for each station using the algorithm derived (Fig. 5b) and then multiplied by their mean density (Fig. 5a) to estimate the biomass (closed symbols and solid line, Fig. 5c). The highest estimated biomass was at the head of the Mississippi trough sites with mean
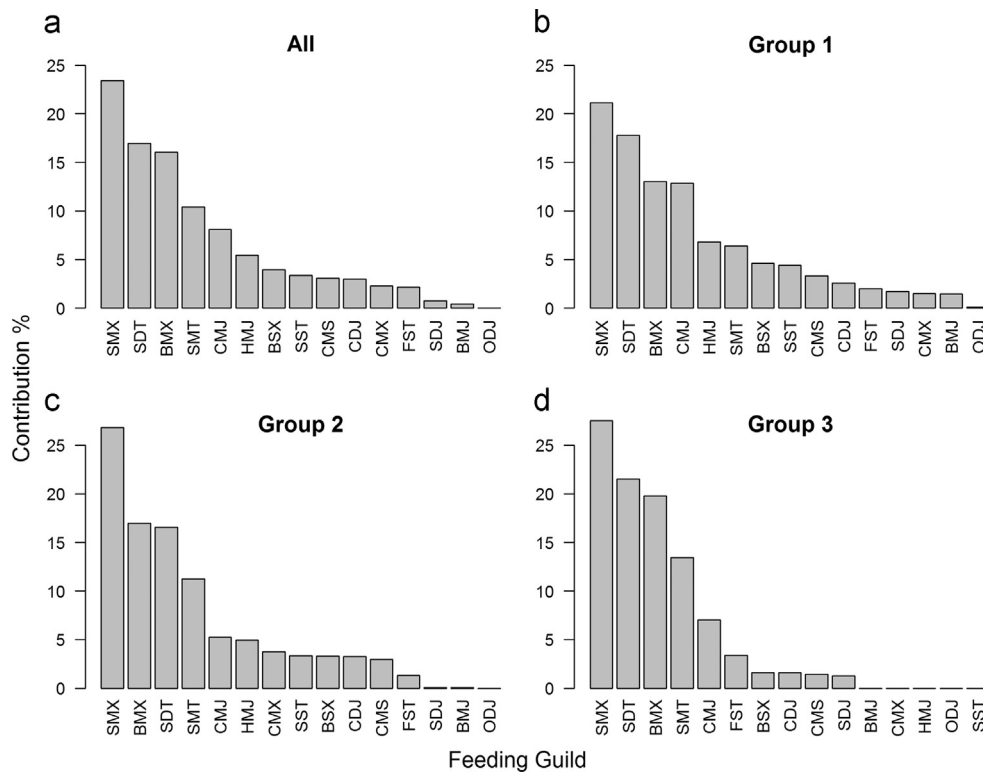
Fig. 4. Accumulated species contribution for each feeding guild type. Average Bray-Curtis similarities for each faunal group were resolved to the contribution of individual species. These species contributions were aggregated across feeding guild type for (a) all DGoMB stations, as well as, for the (b) Group 1, (c) Group 2 and (d) Group 3 stations.

Table 2
Mean dissimilarity between groups shown as a percentage. Statistically significant ($p < 0.01$) groups were defined by SIMPROF by black branches in the cluster diagram.

Groups	Average dissimilarity
Western Group 1 and Abyssal Group 3	81.3
Western Group 1 and Mixed Group 2	76.95
Mixed Group 2 and Abyssal Group 3	90.71

size of 289 (or depth-dependent size of 575) mg C m^{-2} at station MT1, while the lowest was at the abyssal station S4 (9.4 mean size or 0.1 depth-dependent size of mg C m^{-2}). The data point for Station MT1 has been excluded from Fig. 5c in order to avoid grouping of remaining data points towards the bottom of the graph. In the present study, species belonging to the Spionidae and the Paraonidae were the highly dominant taxa within the Central Mississippi trough stations MT1 and MT2, whereas Spionidae, Paraonidae, Maldanidae, Syllidae, Nephtyidae and Cirratulidae were the dominant families overall (supplementary Table S3).

3.4. Diversity indices

From a total sampled area of 0.1725 m^{-2} per replicate the number of species (S) declined significantly with increasing depth ($Y = 74.3 - -16.6 - 0.4X^2$, $R^2 = 0.65$, $F_{2,75} = 72.4$, $p < 0.001$; Fig. 6a). The lowest number of species was 11 at stations B3 and S40 whereas the highest was 96 at station RW1 (Table 3). Species evenness (J') increased significantly with depth ($y = 0.78 + 0.05X - 0.002X^2$, $R^2 = 0.34$, $F_{2,75} = 23.6$, $p < 0.001$) from 0.59 to 0.94, with the highest value at the abyssal station S4 at a depth of 3410 m (Table 3; Fig. 6b). The maximum 'evenness' possible (one) was found at most deep-water sites because almost all individuals represented a different species. Based on 50 randomly selected individuals, the expected number of species E(S_{50}) showed a

significant negative parabolic relationship with depth ($Y = 24.6 + 2.5X - 1.5 \times^2$, $R^2 = 0.31$, $F_{2,75} = 18.1$, $p < 0.001$, Fig. 6c). The E(S_{50}) ranged from 11 at station S40 to 32 at station S35 with the lowest values on the abyssal plain, which were in the order of 16–23 species. This pattern reflects in part a strong spatial variability in polychaete species richness from the shallow to the deepest group of samples. The rarified species diversity declined with depth (Fig. 6a–c).

The number of feeding guilds declined significantly with depth ($Y = 13.8 - 0.9X - 0.2 \times^2$, $R^2 = 0.55$, $F_{2,75} = 47.5$, $p < 0.001$) and was lowest (5) at the abyssal station S4 and highest (15) at the western station RW1 (Fig. 6d). Guild evenness (J') showed a significant parabolic relationship with depth ($Y = 0.67 + 0.13X - 0.02 \times^2$, $R^2 = 0.45$, $F_{2,75} = 31.8$, $p < 0.001$; Fig. 6e). The j' value ranged from 0.58 at WC5 to 0.95 at station B3. The expected number of feeding guilds from randomly selected 50 individuals, E(G_{50}), also showed a significant parabolic relationship with depth ($Y = 8.6 + 1.6X - 0.5 \times^2$, $R^2 = 0.1$, $F_{2,75} = 5.4$, $p = 0.007$, Fig. 6f). The E(G_{50}) varied from 5 at station S4 to 12 at station W3. Fig. 6e and f shows that the numbers of feeding guilds ($p < 0.001$), guild evenness ($p < 0.001$) and expected number of guilds E(G_{50}) ($p < 0.001$) had significant quadratic relationships with depth.

3.5. Polychaete relationships with environmental variables

Using BIO-ENV procedure in PRIMER we identified depth-silt-export POC as a variable combination with the optimum correlation to the biological data ($r_s = 0.44$) (Table 4). The rest of the three successful variable combinations had a slightly lower correlation even though they produced similar correlation coefficients because silt, sand, oxygen, export POC and TPAHWP were correlated with each other ($r_s > 0.32$, $p < 0.001$; $N = 51$ sites). The combination of all other variables, being more normally distributed, produced lower rank correlations.
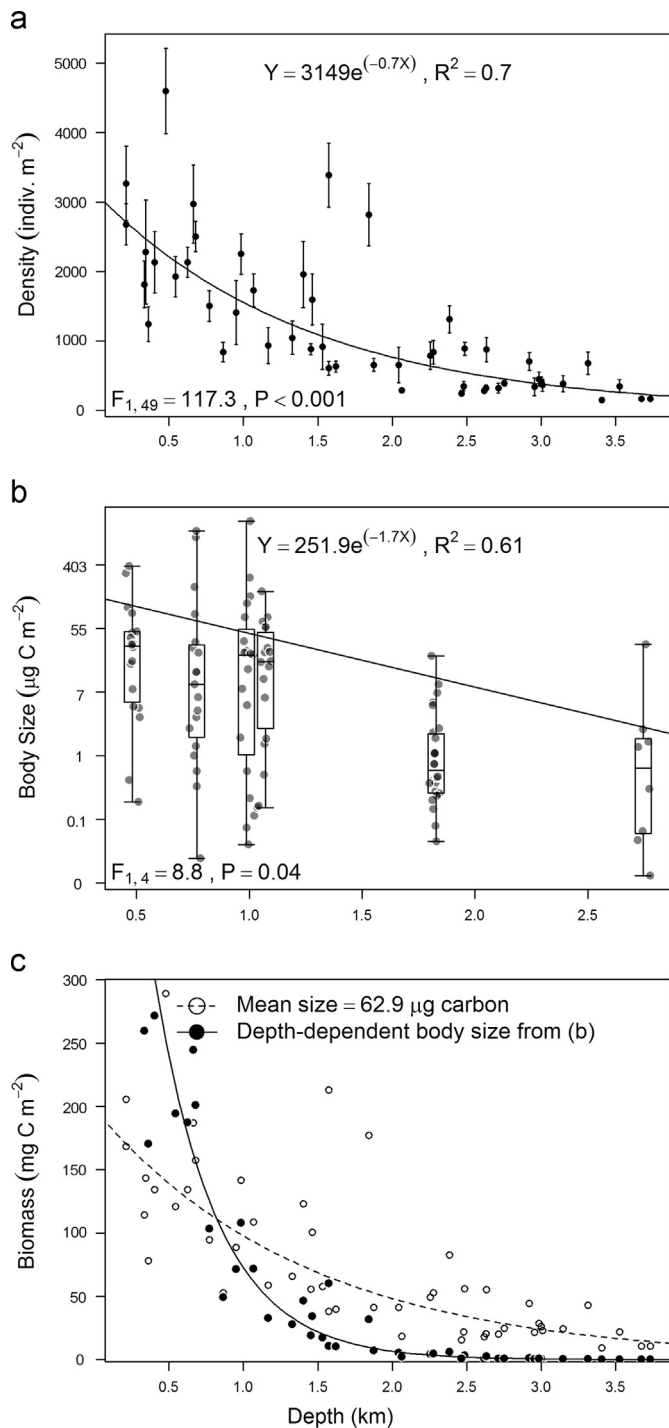
Fig. 5. Polychaete (a) density, (b) body size and (c) biomass as functions of depth. In panel (b), the lower whisker, lower hinge, horizontal line, upper hinge and upper whisker show minimum, lower quartile, median, upper quartile and maximum body size, respectively in Stations MT1, S42, MT3, C7, S36 and MT6.

The PCA ordination (Fig. 7) revealed multivariate environmental properties to be significantly different among the polychaete groups (Fig. 1) defined by cluster analysis (ANOSIM, $R=0.32$, $p=0.001$). The first two principal components explained 63% of total variation in the data (Fig. 7). The first principal component (PC1) was influenced the most by water density (SIGMA), potential temperature (TEMP), silicate (SIO_3), depth, oxygen concentration (O_2), salinity, and export POC flux. The PC2 axis was influenced the most by sediment grain size (% sand, % silt and % clay), total polynuclear aromatic hydrocarbons (PAH's), phosphate (PO_4) and

export POC flux. Along the PC1 axis, Group 1 was separated from Group 2 and Group 3 toward the direction of increasing export POC flux, higher temperature, higher salinity, shallower depth and lower oxygen concentration. Five sites on the east flank of Group 1 correspond to shelf-break stations (W1, WC5, S43, RW1 and S44, Fig. 1). They were characterized by higher temperature and salinity that are associated with the subtropical underwater mass that is transported into the western GoM from the Loop Current (Jochens and DiMarco, 2008). Along the PC2 axis, the north flank of Group 1 (upper and mid slope of the Mississippi and De Soto Canyon areas) was separated from Group 2 and Group 3 due to the finer sediment grain size (higher % silt+% clay) and a higher PAHs concentration. Conversely, Group 2 and Group 3 were characterized by coarser sediment grain size (higher % sand).

4. Discussion

4.1. Polychaete density and biomass in the deep Gulf of Mexico

Typically, deep-sea communities show a trend of decreasing density and biomass with depth (Rowe, 1983; Rex et al., 2006; Wei et al., 2010a). Our analyses of polychaete communities in the northern GoM confirmed some of these trends but revealed some unusual patterns that deserve a more thorough discussion. Our data on density, body size, and biomass of polychaetes from this region are consistent with previous data that suggests a significantly negative exponential relationship with increasing depth. In the GoM, such patterns have been attributed to a decline in photosynthetic carbon sinking to the seafloor and the lateral transport of organic materials across the Mississippi cone from the northern shelf areas onto the deep sediment fan (Goni et al., 1997; Wei et al., 2012). From limited sites on the GoM slope, we showed that the mean size of polychaetes decreased exponentially with depth, suggesting that a decline in food supply with increasing depth not only affected the abundance, but also the body size and consequently the biomass of the polychaete annelids. Applying this depth-dependent relationship to estimate biomass from the mean densities generated a much steeper decline with depth than the trend estimated using an overall mean body size. Both these estimates, however, were not completely accurate. On the one hand, the biomass estimated from mean densities with a fixed body size potentially overestimated the biomass values in deep water. On the other hand, the depth-dependent body sizes probably exaggerated the highest and lowest biomass values. Wei et al. (2012) compared the overall rate of decay (slopes and regression lines) of total macrofaunal density and biomass with depth from 9 benthic surveys in this region. They suggested a shift in the macrobenthic taxonomic composition that was reflected in an increase in smaller taxa (example, nematodes, harpacticoid copepods and ostracods) with depth, the upper slope being dominated by larger macrofaunal taxa and the abyssal plain by smaller 'meiofaunal taxa of macrofaunal size'. Our study suggests that within a single macrofaunal taxon the mean body size may also decrease with depth (example, polychaetes). Morse and Beazley (2008) reported a high organic carbon (OC) content in the upper slope sediments near the head of the Mississippi Submarine Canyon, which corresponds with the high abundance and biomass of polychaetes in this study, suggesting that the observed depth-related patterns are driven by the flux of food to benthic communities.

Numerous studies have demonstrated the role of the Mississippi River in shaping benthic communities (Pequegnat et al., 1990; Rabalais et al., 1996; Wang, 2004). High nutrient inflow leads to high primary productivity that is correlated with the amount of particulate organic matter that eventually reaches the

Table 3
Station, depth (m), total number of individuals (N), total no of species (S), number of individuals m^{-2} (D), Species evenness (J'), expected number of species from randomly selected 50 individuals E(S_{50}), total no of guilds per site, Guild evenness (Pielou's J') and expected number of feeding guilds from randomly selected 50 individuals E(G_{50}). The S, J', E(S_{50}) were based on 3 core replicates per site. Sampled area=0.1725 m^{-2} for each replicate.

Station	Depth (m)	N	S	D (Mean ± SD)	Species evenness (J')	Species E(S_{50})	No of guilds	Guild evenness (J')	Guild E(G_{50})
AC1	2505	21	14	350.1 ± 155.4	0.95	14	9	0.93	9
B1	2260	37	25	786.1 ± 443.3	0.95	25	9	0.84	9
B2	2630	34	21	324.6 ± 89.2	0.93	21	10	0.78	10
B3	2650	22	11	286.4 ± 96.7	0.93	11	6	0.95	6
BH	546	412	83	1925.8 ± 656.3	0.85	29	14	0.77	10
C1	334	210	48	1815.7 ± 748.7	0.88	27	14	0.77	10
C4	1455	204	46	704.9 ± 289.5	0.86	25	13	0.82	10
C7	1080	237	61	889.3 ± 210.1	0.84	27	13	0.82	11
C12	2922	65	26	1597.7 ± 820.4	0.87	22	9	0.83	9
C14	2487	93	28	1730.4 ± 744.4	0.87	22	9	0.84	8
GKF	2452	48	26	247.0 ± 96.4	0.95	26	8	0.85	8
HiPro	1574	412	62	3386 ± 1035.4	0.79	22	13	0.72	9
MT1	481	521	54	3812.7 ± 2286.1	0.76	20	12	0.63	7
MT2	676	525	59	2002.3 ± 1181.4	0.8	23	13	0.73	9
MT3	983	291	67	2253.9 ± 920.9	0.86	28	12	0.83	9
MT4	1401	229	60	1957.1 ± 1067.0	0.87	28	13	0.84	10
MT5	2290	102	31	838.3 ± 381.5	0.9	25	12	0.88	11
MT6	2750	34	20	288.1 ± 224.4	0.92	21	9	0.86	9
NB2	1530	155	53	915.9 ± 731.5	0.87	28	14	0.78	10
NB3	1875	77	35	656.2 ± 205.8	0.87	26	11	0.9	10
NB4	2030	72	31	655.1 ± 571.5	0.88	25	12	0.88	11
NB5	2070	39	14	292.2 ± 57.5	0.91	14	6	0.82	6
RW1	213	372	96	2679.4 ± 662.4	0.86	31	15	0.78	11
RW2	950	189	57	1411.0 ± 1032.0	0.83	26	14	0.82	11
RW3	1320	159	55	1047.0 ± 536.3	0.83	27	12	0.84	11
RW4	1570	173	53	607.5 ± 220.0	0.85	26	10	0.91	10
RW5	1620	81	28	633 ± 178.2	0.85	21	10	0.8	9
RW6	3015	74	23	365.2 ± 191.7	0.88	19	11	0.83	10
S1	3528	41	16	347.8 ± 131.2	0.96	16	7	0.93	7
S2	3732	22	14	171.0 ± 20.5	0.95	14	8	0.9	8
S3	3675	24	18	153.6 ± 20.5	0.95	18	8	0.87	8
S4	3410	18	12	149.3 ± 70.9	0.97	12	5	0.94	5
S5	3312	66	27	681.2 ± 225.5	0.9	23	11	0.84	10
S35	658	321	87	2973.9 ± 1259.2	0.89	32	14	0.82	10
S36	1850	399	66	2816.9 ± 1549.5	0.78	24	13	0.81	10
S37	2388	195	47	1312.5 ± 439.1	0.83	23	13	0.77	9
S38	2635	95	33	876.5 ± 397.6	0.87	24	12	0.86	11
S39	3007	46	27	415.1 ± 146.7	0.95	27	11	0.85	11
S40	2975	14	11	272.5 ± 272.3	0.91	11	9	0.89	9
S41	2982	39	17	362.3 ± 307.1	0.91	16	9	0.86	9
S42	773	165	50	1353.0 ± 783.1	0.91	27	13	0.84	11
S43	366	140	57	1244.1 ± 561.9	0.9	31	13	0.79	10
S44	215	316	74	3268.4 ± 1189.7	0.81	27	14	0.74	10
W1	379	431	67	2133.3 ± 985.4	0.66	19	13	0.64	8
W2	625	279	84	1706.7 ± 1026.5	0.81	29	14	0.81	11
W3	860	145	55	840.6 ± 314.5	0.88	30	14	0.84	12
W4	1420	91	32	882.3 ± 175.3	0.86	22	11	0.88	10
W5	2755	34	15	391.9 ± 86.3	0.95	15	8	0.9	8
W6	3140	68	26	386.1 ± 263.4	0.93	23	10	0.89	10
WC12	1168	78	35	934.5 ± 577.4	0.92	28	10	0.85	9
WC5	400	601	72	2281.7 ± 1674.4	0.59	19	12	0.58	8

seafloor, providing food for benthic fauna. Our study of polychaetes is consistent with the decrease in macrofaunal density with depth. In addition, we show that density in the Mississippi Trough was higher than in the eastern and western regions that presumably lack a steady inflow of nutrients.

4.2. Polychaete community structure and its relationship with environmental variables

The low diversity observed on the abyssal plain can be explained by a diminished food supply, which ultimately results in low environmental disturbance, low growth-rates and low rates of competitive displacement (Cosson-Sarradin et al., 1998). Our results support the conclusions of many deep-sea studies conducted in other areas, which suggest that the environmental processes that control diversity patterns could ultimately be taxon

specific as well as locality specific (Paterson et al., 1994; Wei et al., 2010b). Evidence from species and feeding guild data suggests that the polychaete assemblages that characterize the three faunal groups (Western Group 1, Mixed Group 2 and Abyssal Group 3) are a result of specific bottom-water dynamics, which clearly mark a difference between shallow-water and deep-sea systems (Rabalais et al., 1996). These three faunal groups were influenced by variations in depth, oxygen, salinity, sediment characteristics and export POC. Variation in inputs of organic material in the deeper region of the GoM may be one of the most important drivers of species and feeding guild diversity (Wang, 2004). The majority of motile polychaete species, belonging to feeding guilds SMX, SMT and BMX occupied the areas nearest to the mouth of the Mississippi river. This tidally dominated delta region displays strong ebb and flood currents and is made up of mainly soft and silty sediments, characterized by the slumping of recently
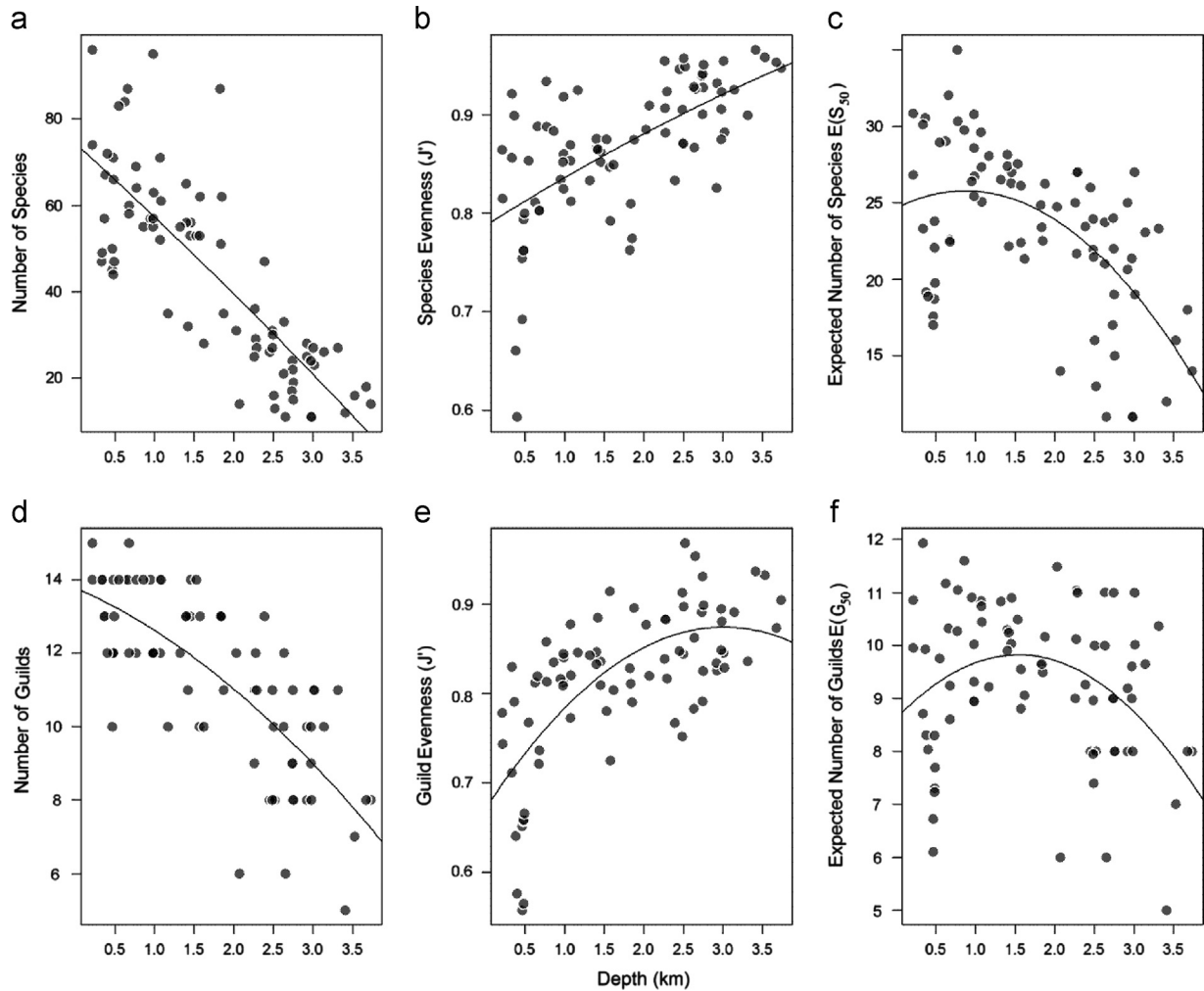
Fig. 6. Polychaete (a) number of species, (b) species evenness (J'), (c) expected number of species from 50 randomly selected individuals E(S_{50}), (d) number of feeding guild, (e) guild evenness (J'), (f) expected number of feeding guild from 50 randomly selected individual E(G_{50}) as functions of depth.

Table 4
Results from BIO-ENV showing Spearman rank correlations (r_s) observed between polychaete and environmental matrices and the level of significance for each best variable combination.

No of variables	Best combination of variables	r_s	p
3	Depth-silt-export POC	0.44	< 0.001
3	Depth-oxygen-silt	0.42	< 0.001
3	Depth-sand-export POC	0.41	< 0.001
3	Depth-silt-TPAHWP	0.41	< 0.001
4	Depth-oxygen-silt-export POC	0.41	< 0.001
4	Depth-relative fluorescence-silt-export POC	0.41	< 0.001
4	Depth-sand-silt-export POC	0.41	< 0.001
4	Depth-relative fluorescence-oxygen-silt	0.4	< 0.001
5	Depth-relative fluorescence-oxygen-silt-export POC	0.41	< 0.001
5	Depth-oxygen-pm-silt-export POC	0.4	< 0.001

Note: Units for environmental variables are: Depth (m), Temperature (°C), Salinity (PSU), Sigma-theta (kg/m³), Relative Fluorescence (volts), POC (ug C/L), DO (mg/L). *Abbreviation*: POC (Particulate Organic Carbon in sediments); % Silt (Percentage of silt in sediments); % Clay (Percentage of clay in sediments); DO (Dissolved Oxygen in the bottom water); TPAHWP (Total Polynuclear Aromatic Hydrocarbons with Perylene in mg g^{-1}).

deposited material from the shelf and the slope. SMX, SDT, BMX, SMT and CMJ, the main feeding guilds observed across the Gulf, were made up of species like *Litocorsa antennata*, *T. marioni*,

P. monilaris and *Cossura delta*, which were found in high densities at almost all depths sampled during the DGoMB program. Thriving in soft sediments, these taxa are known to be dominant in the deep sea under low-oxygen conditions (Beesley et al., 2000). In our study polychaete species belonging to the families of Cirratulidae, Paraonidae, Syllidae and the Spionidae were some of the dominant taxa in the GoM. These have been previously reported to be well represented in bathyal and abyssal environments (Fauchald and Jumars, 1979) and respond quickly to gradients in organic enrichment or stressed bathyal settings (Demaster et al., 1994; Levin and Gage, 1998). Tentaculate cirratulid polychaetes of the genus *Tharyx* are extremely abundant in estuarine high salinity and polluted areas. These taxa, which represent the SMT feeding guild, are typically one of the largest contributors of macrofaunal species in the deep sea (Jumars, 1975) and were found in significant numbers at sites on the upper continental slopes across the GoM.

The stable areas of the continental slope between depths of 2000 and 3000 m were not affected by the slumping of organic-rich material were dominated by the SDT-feeding polychaetes *Prionospio cirrifera*, *P. cristata* and *P. ehlersi* species that use specialized palps to construct tubes from mud grains (Fauchald and Jumars, 1979). The habitat-structuring capacity of tube builders enables them to create a complex microhabitat, which is believed to be an important driver of diversity and density of the macrobenthos (Van Hoey et al., 2006). In high densities tube
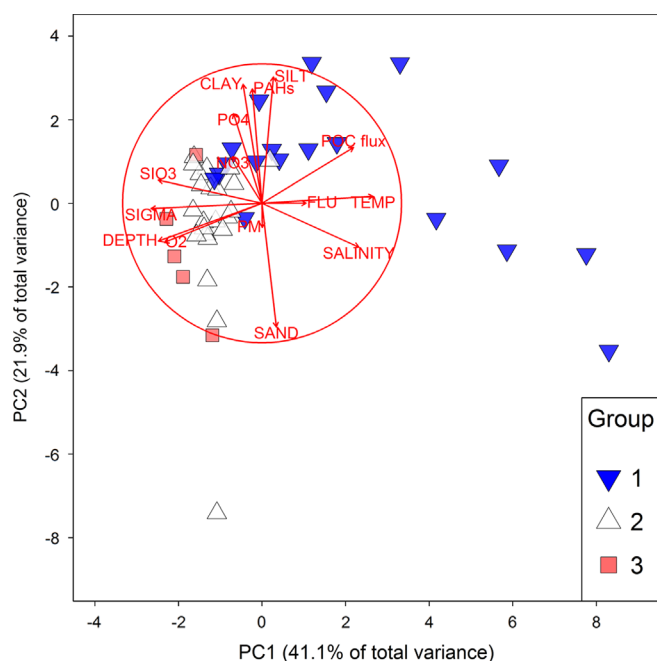
Fig. 7. Principal component analysis (PCA) showing ordination of seafloor environmental properties. The symbols indicate significant faunal group. The arrows indicate environmental Eigen vectors on the PC1 and PC2 axes. The large circle indicates that the sum of squared Eigen vectors equals 0.5.

patches may trap suspended organic material, a vital source of food for deep-sea benthic macrofauna (Bailey-Brock, 1984; Friedrichs et al., 2000). A number of other tube-dwelling species like *Maldane* sp. A, *Myriochele heeri*, *Myriochele* sp. A, *Myriowenia* sp. A, *S. berkeleyorum,* and *Sarsonuphis hartmanae* were also found in high densities in Group 2. This group comprised species with different types of feeding apparatus and mobility, an indication of opportunistic feeding habits that maintain high diversity by reducing interspecies competition for resources in a region where food supply is mostly uncertain (Escobar-Briones and García-Villalobos, 2009; Rowe and Kennicutt II, 2009).

4.3. Patterns of polychaete species diversity and functional groups in the deep Gulf of Mexico

The absence of a mid-depth maximum (MDM) in species diversity may be related to the complex topographic features and hydrographic processes that influence dispersal and small-scale geographic isolation of species. On the other hand, the MDM-like patterns observed in the feeding guild datasets most likely depend on factors such as habitat conditions, disturbance and inter-specific competition (Pinedo et al., 1997). Due to the vast area sampled in the GoM, the MDM-like pattern observed in the DGoMB feeding guild dataset requires further evaluation, as these patterns may also be a reflection of the area being sampled. Many of the species observed in our study were confined to specific depth ranges (isobaths) or to particular physiographic features within depth ranges (Fig. 1). For example, high species numbers were observed at the BH and WC5 sites located close to the basin and non-basin areas around the mouth of the Mississippi. Similarly, sites located on the Florida and Sigsbee escarpments showed some of the highest species numbers for these areas.

By determining the number of species that form a feeding guild, we can estimate the degree of functional redundancy that may be important to ecosystem resiliency (Walker, 1995). Most studies agree that a decrease in the flux of organic carbon can result in a corresponding decrease in species abundance, thereby decreasing dominance and increasing diversity (Levin and Gage, 1998; Granberg

et al., 2008; Morse and Beazley, 2008; Escobar-Briones and García-Villalobos, 2009). In the GoM, high values of organic carbon (≥ 1.0 wt%) were found in the top 2 cm of sediment from stations MT1, MT3, HiPro, S35 and BH (Morse and Beazley, 2008). These sites also had the highest mean carbon biomass and species richness (Table 3). These high richness values are not representative of the nominal diversity at these sites and could most likely reflect a contribution of species dispersing from denser more diverse populations around the Mississippi trough. With a considerably higher influence of the Mississippi River and Fan on these sites, Wei et al. (2010a) showed that organic input in the form of river-borne material from the Mississippi River, or enhanced primary production, causes an east–west gradient in faunal composition and richness, which could also contribute to these local differences in species richness and diversity.

Our results used the 30% similarity level to differentiate between different groups based on species composition (Fig. 2; Table 1) but some degree of similarity among stations merely reflected the presence of a few cosmopolitan species, for example, *Prionospio cristata* which occurred at most stations (Table S2 under supplemental information). The nMDS data on feeding guilds and PCA analysis indicated the composition of polychaete feeding guilds to be highly affected by a range of environmental gradients. The most significant environmental gradient was a result of the bottom sediment dynamics of the Mississippi trough where the cone is composed of soft sediments, the central and northern areas are made up of a mixture of thick and soft sediments, and eastern regions show the presence of carbonate sediments.

Additionally, analysis of feeding guilds based on the DGoMB dataset provides us with insights into polychaete food sources and polychaete interactions within the deep-sea environment, for example, the very mechanism of transporting food from the environment into the organism (Fauchald and Jumars, 1979). Thus, feeding guild diversity can be used as a proxy for ecosystem function when assessing the impact of natural and anthropogenic disturbances on benthic communities (Brown et al., 2000; Pacheco et al., 2011; Wagner and Barros, 2011). In our case, Group 2 had the highest number of feeding guilds, including carnivores, herbivores and surface and subsurface deposit feeders, suggesting a wide variety of food resources and diverse pathways of energy and matter (Ulanowicz, 1997). Species diversity and feeding guild diversity were higher on the upper and mid slopes of the Mississippi trough than in the deeper regions, suggesting that food resources are an important driver of both taxonomic and functional diversity. The deeper areas of the lower slope and the abyssal plain were dominated by carnivorous motile feeders (i.e., CMJ) and the surface and subsurface motile deposit feeders, such as BMX, SMX and SMT. The flux of variable food particles at feeding sites allows for the use of jaws, tentacles and unarmed proboscides. These structures facilitate the capture of a much wider range of food types, reducing dependency on suspended organic matter. Motile jawed carnivores (CMJ) constitute one of the major categories of polychaetes in the deep-water areas (Fauchald and Jumars, 1979) and include most scale worms (except some polynoids falling in this category, as they are usually described as 'sit-and-wait predators'). A majority of the motile benthic carnivore species found on the lower slope and abyssal plain belonged to the families of the Amphinomidae, Chrysopetalidae, Dorvilleidae, Glyceridae, Goniadidae, Lumbrineridae, Nereidae, Paralacydoniidae, Phyllodocidae, Pilargiidae and Syllidae. According to Fauchald (1977) sessile polychaetes usually have a larger 'catch-apparatus' than motile ones, and such an apparatus would be uneconomical in nutrient-poor, deep-water environments (Fauchald and Jumars, 1979). Low levels of food in the deep-sea probably contribute to a higher incidence of predation and a selection against other food capturing strategies (Fauchald and Jumars, 1979; Fauchald and Rouse, 1997; Rouse and Pleijel, 2001).

This study was limited by information and data on the qualitative input of food-supply to the deep benthos. As many researchers have acknowledged, the growth potential of deep-sea taxa using assimilable organic carbon (AOC) versus refractory organic carbon compounds that are highly responsible for the long-term sequestration of organic content in sediments supporting benthic life (Aller et al., 2002; Wieking and Kröncke, 2005; Shields and Hughes, 2009). We hope future studies on deep-sea benthic macrofauna in the GoM will incorporate the importance of the quality of organic carbon compounds.

Species identification of deep-sea, sediment-dwelling polychaetes can be problematic. Specimens are usually small and fragile and often not in an optimal condition after sediment processing. Furthermore, the taxonomic literature is often limited, causing many species to remain unnamed. Some authors have suggested addressing this problem by conducting their analysis on higher taxonomic levels, such as families, a strategy termed "taxonomic sufficiency" (Maurer, 2000; Narayanaswamy et al., 2003; Domínguez-Castanedo et al., 2007; Terlizzi et al., 2008; Bacci et al., 2009). Nevertheless, Linnaean taxonomic ranks are subjective and analytical results may vary depending on the family definition adopted (Warwick and Somerfield, 2008). Polychaete feeding guilds can be easily defined on the basis of morphological structures, allowing for a more objective method of classifying animals and at the same time providing insights into functional diversity. Additionally, with competing species having the ability to vary their food resources, feeding behavior will help in understanding the processes of ecological succession and speciation in a region governed by limited food resources (Rouse and Pleijel, 2001; Pagliosa, 2005; Domínquez-Castanedo et al., 2012).

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2013.07.002.

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