Vol. 561: 51–68, 2016
doi: 10.3354/meps11905

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 15

Impacts of the *Deepwater Horizon* oil spill on deep-sea coral-associated sediment communities

Amanda W. J. Demopoulos[1,*], Jill R. Bourque[1], Erik Cordes[2], Katherine M. Stamler[3]

[1]US Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL 32653, USA
[2]Temple University, Philadelphia, PA 19122, USA
[3]Cherokee Nation Technology Solutions, contracted to the US Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL32653, USA

ABSTRACT: Cold-water corals support distinct populations of infauna within surrounding sediments that provide vital ecosystem functions and services in the deep sea. Yet due to their sedentary existence, infauna are vulnerable to perturbation and contaminant exposure because they are unable to escape disturbance events. While multiple deep-sea coral habitats were injured by the 2010 *Deepwater Horizon* (DWH) oil spill, the extent of adverse effects on coral-associated sediment communities is unknown. In 2011, sediments were collected adjacent to several coral habitats located 6 to 183 km from the wellhead in order to quantify the extent of impact of the DWH spill on infaunal communities. Higher variance in macrofaunal abundance and diversity, and different community structure (higher multivariate dispersion) were associated with elevated hydrocarbon concentrations and contaminants at sites closest to the wellhead (MC294, MC297, and MC344), consistent with impacts from the spill. In contrast, variance in meiofaunal diversity was not significantly related to distance from the wellhead and no other community metric (e.g. density or multivariate dispersion) was correlated with contaminants or hydrocarbon concentrations. Concentrations of polycyclic aromatic hydrocarbons (PAH) provided the best statistical explanation for observed macrofaunal community structure, while depth and presence of fine-grained mud best explained meiofaunal community patterns. Impacts associated with contaminants from the DWH spill resulted in a patchwork pattern of infaunal community composition, diversity, and abundance, highlighting the role of variability as an indicator of disturbance. These data represent a useful baseline for tracking post-spill recovery of these deep-sea communities.

KEY WORDS: Cold-water corals · Oil spill · Sediment communities · *Deepwater Horizon* · Macrofauna · Meiofauna

INTRODUCTION

Between April and July, 2010, approximately 3.19×10^6 barrels (134 million gallons; 507 million liters) of oil were released into the Gulf of Mexico (GOM) from the Macondo well at 1500 m depth as a result of the *Deepwater Horizon* (DWH) blowout (USA v. BP et al. 2015). The oil was present in surface sheens, in a massive deep-water plume (Camilli et al. 2010), and deposited on the seafloor over a large area (3200 km^2; Valentine et al. 2014, Chanton et al. 2015). The addition of the 1.84 million gallons (6.97 million liters) of the dispersant Corexit® released in surface waters and at depth further dispersed oil into the water column where natural hydrographic stratification retained oil-derived particles at depth, limiting vertical transport to the surface (Camilli et al. 2010, Valentine et al. 2014, White et al. 2014). Occurring at

*Corresponding author: ademopoulos@usgs.gov

extreme depths, the DWH spill was unlike any previous spill (Peterson et al. 2012) and presented unique challenges to the assessment of injuries to remote deep-sea communities.

Deep-sea sediment meiofauna and macrofauna (infauna) are important components of benthic biodiversity, and provide essential ecosystem functions including transference of energy that reaches the seafloor to higher trophic levels, sediment bioturbation and stabilization, and organic matter decomposition (Gage & Tyler 1991, Danovaro et al. 2008, Gray & Elliott 2009, Thurber et al. 2014). However, due to their low mobility and relatively inactive lifestyles, infaunal communities are sensitive to ecological perturbations, such as hydrocarbon contamination (Warwick 1981, Fleeger & Chandler 1983, Montagna & Harper 1996, Montagna & Li 1997) and organic enrichment (Pearson & Rosenberg 1978, Gray et al. 1979, Weston 1990). Meiofauna typically have short generation times and can respond rapidly to contaminant exposure, resulting in populations rebounding over shorter time periods relative to macrofauna (Heip et al. 1985). However, this response is taxon specific; nematodes are generally more tolerant of oil contamination (Giere 1979), whereas harpacticoid copepods are more sensitive to contaminant exposure (Carman & Todaro 1996, Bejarano et al. 2006, Bang et al. 2009, Veiga et al. 2010). Given their different responses to organic enrichment and pollution, the nematode to copepod ratio (N:C) has been used as an indicator of oil exposure (Raffaelli 1987, Montagna et al. 2013, Baguley et al. 2015), albeit with some notable limitations (Ansari & Ingole 2002, Veiga et al. 2010). While N:C can be influenced by non-pollution vectors, such as temporal changes in food supply and predation pressure (Coull et al. 1981, Lambshead 1984), the metric has been useful in identifying areas of oil-spill impact in the deep sea (Baguley et al. 2015).

Macrofaunal communities generally exhibit decreased diversity and increased dominance of opportunistic taxa following organic enrichment and pollution exposure (Pearson & Rosenberg 1978, Gray et al. 1979). Specific taxa used as pollution indicators include the polychaete families Capitellidae, Cirratulidae, and Spionidae, due to their ability to rapidly colonize substrates and their high tolerance to oil exposures (Gomez Gesteira et al. 2003, Dean 2008). In contrast, Amphipoda (Crustacea) have been used as indicators of community change resulting from oil pollution (Gesteira & Dauvin 2000, Grant & Briggs 2002) and for toxicity tests (Carr et al. 1996, Ho et al. 1997), due to their sensitivity to oil exposure. Severe disturbance also can lead to high variability in populations and communities, as follows from Schmalhausen's law, which states that species already living in stressful environments or at their tolerance boundaries are more susceptible to even small environmental changes (Lewontin & Levins 2000). For infauna, increased variability in the density, diversity, and multivariate dispersion of macrofaunal communities has been used as a metric to track benthic community response to oil contamination (Gray et al. 1990, Warwick & Clarke 1993).

Soft-sediment benthic communities in the deep GOM have historically been well-studied (Rowe et al. 1974, Pequegnat et al. 1990, Baguley et al. 2006a, 2006b, Rowe & Kennicutt 2009, Wei et al. 2010, Carvalho et al. 2013), although information from directly near the wellhead prior to the spill is limited. Natural seafloor hydrocarbon seepage is present throughout the GOM (MacDonald et al. 1996, 2002), resulting in low and patchy background polycyclic aromatic hydrocarbon (PAH) concentrations in soft-sediments (0 to 1033 ng g^{-1}; Wade et al. 2008, Rowe & Kennicutt 2009). Deep-sea macrofaunal community structure in the GOM is a function of multiple factors, including geographic location and depth. Density and biomass generally decrease with depth in response to declining concentrations of surface-derived phytodetritus, whereas diversity reaches a maximum at intermediate depths (1200 to 1600 m), and the eastern and western GOM have distinctly different communities (Haedrich et al. 2008, Rowe & Kennicutt 2009, Wei et al. 2010, 2012). Meiofauna follow similar patterns, with localized increases in density and biomass near the Mississippi Canyon (Baguley et al. 2006a, 2008).

Impacts of the DWH oil spill have been reported for deep-sea soft sediment habitats (Montagna et al. 2013, 2016, Baguley et al. 2015, Qu et al. 2015). The spatial extent of impact to infauna was estimated to be 172 km^2 (Montagna et al. 2013), with high and moderate impacts found within 3 and 17 km from the wellhead, respectively. Expanding on the work of Montagna et al. (2013), Baguley et al. (2015) analyzed 8 additional stations, and concluded that the areal extent of impact was much larger (309.7 km^2). This area corresponded to the purported shape of the deepwater plume (Camilli et al. 2010), trending in a NE to SW direction. Decreased macrofaunal (>300 µm) and meiofaunal (>45 µm) diversity and increased N:C ratios corresponded to spill-associated contaminants including barium and hydrocarbons (Montagna et al. 2013). High dominance of nematodes and low meiofaunal diversity were associated with organic enrichment and toxicity (Baguley et al.

2015). Declines in overall abundance and diversity, and increased densities of carnivorous taxa were observed in polychaete assemblages located near the wellhead (5 to 9 km; Qu et al. 2015) compared to historical data (Rowe & Kennicutt 2009, Wei et al. 2010, Carvalho et al. 2013). However, these studies were limited to the soft sediment environments and did not investigate other habitats in the GOM, such as deep-sea corals and cold seeps, where environmental controls on these distinct sediment communities may differ (e.g. Demopoulos et al. 2014, Bourque et al. 2016).

DWH-associated injuries to deep-sea corals and surrounding sediments have been described (Fisher et al. 2014a). At a coral habitat located in the Bureau of Ocean Energy Management (BOEM) lease block MC294 (see Fig. 1), an unusual brown flocculent material containing Macondo oil and dispersant residues was found loosely attached to corals in November and December 2010, and various pathologies and abnormalities in the corals and their ophiuroid associates were observed and quantified (White et al. 2012, Fisher et al. 2014b, Girard et al. 2016). DWH oil spill-derived compounds, including Macondo oil and dispersant, also were present in sediments adjacent to corals at MC294 and MC344 (White et al. 2012, 2014). Two additional sites, identified within BOEM lease blocks MC297 and MC344 also contained oil spill-impacted coral colonies (Fisher et al. 2014b). Overall, the injury to corals at MC294, MC297, and MC344 exceeded naturally occurring levels observed at a reference site within AT357 (Hsing et al. 2013, Fisher et al. 2014b).

Impacts from DWH have been reported for sediment communities in proximity to deep-sea coral colonies only at one site, MC294 (Fisher et al. 2014a). Macrofaunal communities at the impacted site MC294 differed from those adjacent to healthy corals at MC507 and AT357. Sediment communities at MC294 exhibited high variability in macrofaunal densities, overall low diversity, and a low proportion of crustaceans as compared to healthy coral sites (Fisher et al. 2014a). High meiofaunal densities were observed at MC294 in 2010 immediately after the spill, while densities at both the impacted and healthy coral sites in 2011 were significantly lower than those found in background GOM soft-sediment (Baguley et al. 2006a, Rowe & Kennicutt 2009). While Fisher et al. (2014a) focused on the oil-spill impact to infaunal communities at MC294, no studies to date have quantified the extent of the spill impacts to sediment communities at other deep-sea coral sites in proximity to DWH.

The depositional environment and associated hydrodynamic regime around coral habitats differ from the extensive expanses of soft-sediments that dominate the sea floor of the GOM (e.g. Mienis et al. 2007, 2009, 2012), and thus injuries stemming from the DWH oil spill within these coral habitats may not manifest in the same way as in soft-sediment environments. In addition, given that the infaunal communities associated with deep-sea coral sediments differ from those in other soft-sediment environments in the GOM (Demopoulos et al. 2014, Fisher et al. 2014a), the patterns of community response to the spill may also differ. The purpose of this study was to estimate the oil-spill impact to multiple sediment communities associated with deep-sea corals located at various distances and directions from the wellhead. This study was one component of a larger research program to assess the impact of the DWH oil spill to deep-sea environments and was conducted under the leadership of the DWH Natural Resource Damage Assessment (NRDA) Deepwater Benthic Communities Technical Working Group. For this study, we tested the following hypotheses: (1) Distinct differences in macrofaunal and meiofaunal community metrics, including density, diversity, composition, and variability in these metrics, will be associated with differing concentrations of contaminants in sediments (e.g. hydrocarbons, barium). (2) The relative magnitude of injury to coral-associated sediment fauna declines with distance from the wellhead.

MATERIALS & METHODS

Study locations

Sediments were collected adjacent to deep-sea octocoral habitats at 13 locations within 8 sites in the northern GOM (Table 1, Fig. 1). Site names correspond to the BOEM Lease Block designations, with individual sampling locations within a site designated A, B, and C (Table 1). Site locations ranged in depth from 888 to 1857 m, and were 6 to 183 km from the DWH wellhead. Octocoral assemblages at each site were composed primarily of either *Paramuricea biscaya* (the most commonly injured species in the spill) or the closely related *Paramuricea* sp. B3 (Doughty et al. 2014, Quattrini et al. 2014), along with *Bathypathes* sp., *Chrysogorgia* sp., *Clavularia rudis*, Keratoisidinae bamboo corals, and/or *Paragorgia regalis* (Table 1).

Table 1. Sampling locations for assessment of impacts of the *Deepwater Horizon* (DWH) oil spill on deep-sea coral-associated communities, showing habitat characteristics, geographical coordinates, and the number of samples used for each analysis. MF: macrofauna; ME: meiofauna; HC: hydrocarbons; MT: metals; SC: sediment chemistry

Location	Depth (m)	Corals present	Distance from DWH (km)	Lat.	Long.	MF	ME	HC	MT	SC
MC297A	1550	*Paramuricea biscaya*	6	28.69606	−88.34633	4	3	2	1	1
MC297B	1586	*Paramuricea biscaya*	6	28.68222	−88.34502	3	3	3	1	1
MC297C	1578	Dead octocorals	6	28.68136	−88.34402	3	3	2	1	1
MC294A	1372	*Paramuricea biscaya* *Paragorgia regalis*	13	28.67213	−88.47643	3	3	3	1	1
MC294B	1372	*Paramuricea* sp. B3	13	28.67222	−88.47638	3	3	2	1	1
MC118B	888	*Bathypathes* sp. *Paramuricea biscaya* *Clavularia rudis*	18	28.85595	−88.49361	3	3	2	1	1
MC344A	1857	*Paramuricea biscaya* Keratoisidinae sp. I2	22	28.63381	−88.16969	3	3	2	1	1
MC344B	1857	*Paramuricea* sp. B3	22	28.63359	−88.16952	3	3	2	1	1
MC203A	919	*Paramuricea* sp. B3	28	28.78727	−88.63471	3	3	2	1	1
MC036A	1094	*Paramuricea* sp. B3 *Chrysogorgia* sp. 1B	27	28.93541	−88.20138	3	3	2	1	1
MC036B	1094	*Paramuricea* sp. B3	27	28.93538	−88.20265	3	3	2	1	1
MC507A	1043	*Paramuricea* sp. B3	55	28.48550	−88.85084	3	2	2	1	1
AT357B	1048	*Paramuricea* sp. B3	183	27.58663	−89.70406	3	3	2	1	1

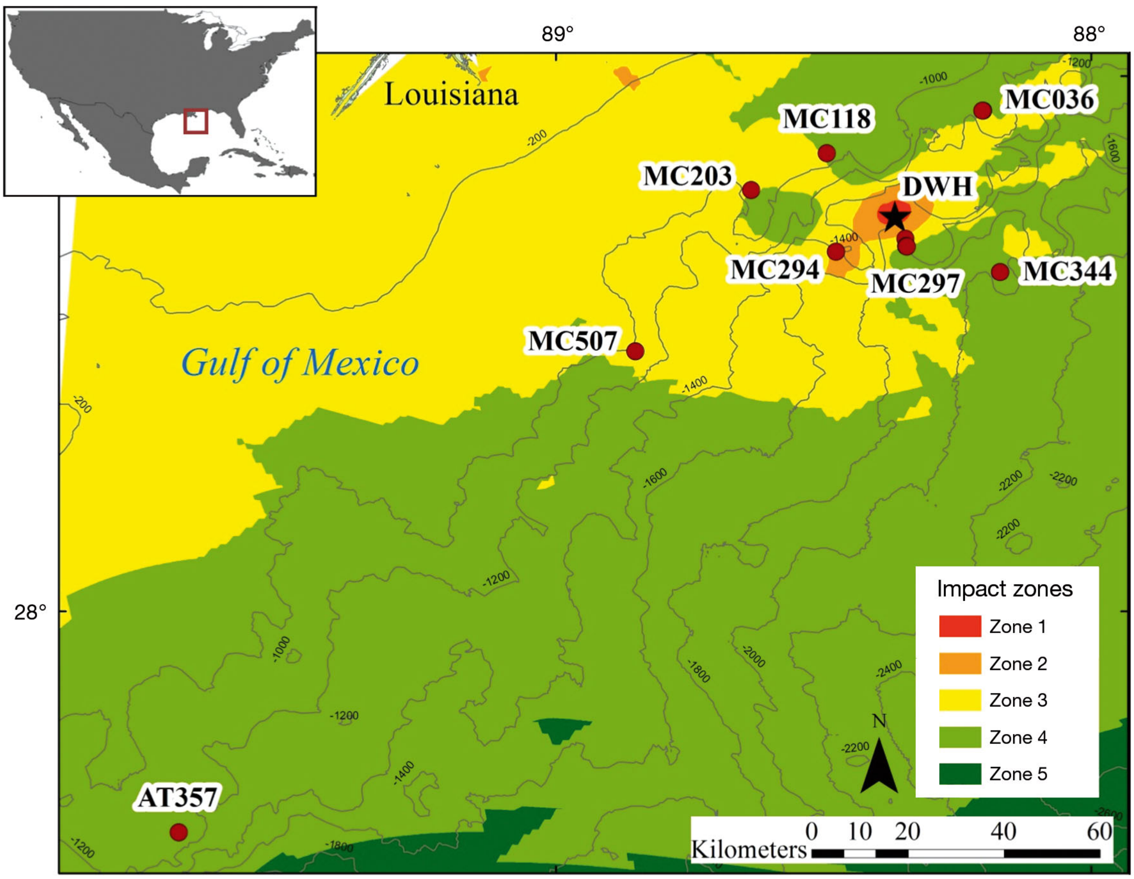

Fig. 1. Locations of coral sites sampled in 2011 in the northern Gulf of Mexico, showing the location of the *Deepwater Horizon* (DWH) wellhead (★) and extent of impact zones, defined by Montagna et al. (2013) based on soft-sediments collected in 2010

Sampling methods

Sediment samples were collected in 2011 aboard the *Holiday Chouest* (4 to 23 October 2011 cruise), implemented as part of the NRDA response to the DWH oil spill. Push cores (6.35 cm diameter) were collected adjacent to coral colonies (within 1 m) using a remotely operated vehicle (ROV) (Fig. 2). At each sampling location, 3 to 4 cores were processed for infauna analysis, 2 to 3 cores for hydrocarbon analysis, 1 core for metals analysis, 1 core for sediment geochemistry, and 1 core for organic composition (Table 1). All sediment cores were sectioned vertically (0–1, 1–3, 3–5 and 5–10 cm) after recovery. Sediment-core sections processed for infaunal analysis were preserved whole in 10% buffered formalin solution until they were returned to the laboratory where they were washed through a 300 µm and 45 µm mesh sieve series to separate out macrofauna (>300 µm) and meiofauna (>45 µm). Macrofauna were subsequently stored in 80% ethanol and meiofauna in 8% formalin. Quantifying both size classes from the same core and not from separate subcores (e.g. Rowe & Kennicutt 2009) reduces small-scale variability among cores inherent in deep-sea samples (Gage & Tyler 1991). Macrofauna were sorted with a dissecting microscope and identified to the lowest taxonomic level possible, including family level for polychaetes, oligochaetes, peracarid crustaceans, and aplacophorans. Family level identification has been found to be sufficient for oil-spill impact assessments on sediment fauna (Gomez Gesteira et al. 2003) and our procedure is comparable to previous studies (Montagna et al. 2013). Meiofauna were extracted from the sediment using the Ludox® density gradient centrifugation technique (Burgess 2001), sorted with a dissecting microscope, and identified to order level or higher. Sediment sections from cores for geochemistry analysis were frozen whole at –20°C until returned to the lab. Grain size analysis was performed on these cores using the Folk method (Folk 1968). Sediment sections for hydrocarbon (EPA Methods 8270M and 8015M), metals (EPA Method 6020), and organic composition analyses were processed by Alpha Analytical Labs, resultant data from which were downloaded from the NRDA DIVER website (available at https://dwhdiver.orr.noaa.gov/) on December 9, 2013. Concentrations of contaminants were assumed to be zero if values were below the detection limit.

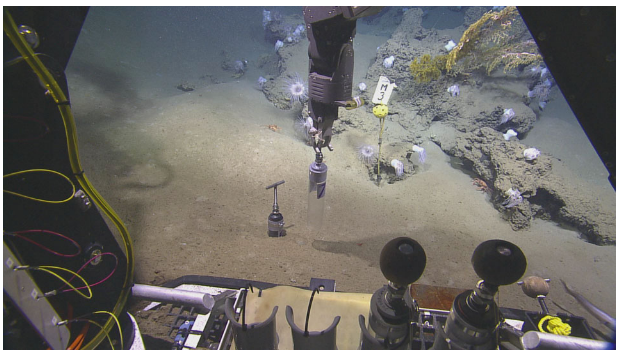

Fig. 2. Sediment sample collection near *Paramuricea biscaya* coral colonies at site MC297 in the northern Gulf of Mexico to assess the impact of the DWH oil spill. Photo credit: OET, 26 June 2013

Data analysis

This study presents a complete data set of meio- and macrofauna as well as key geochemical parameters from the top 3 cm of the sediment cores. Macrofaunal community data for the 0–10 cm fractions and meiofaunal community data for the 0–3 cm fraction from MC294, MC507, and AT357 were previously reported in Fisher et al. (2014a). Hydrocarbon concentrations, including total saturated hydrocarbons (SatHC) and polycyclic aromatic hydrocarbons (Tox50, the sum of 53 PAHs; see Table A1 in the Appendix), from the 0–1 and 5–10 cm fractions from MC294, MC507, and AT357, were also reported in Fisher et al. (2014a). Natural sediment deposition rates in the northern GOM are typically low, ranging from 0.04 to 0.44 cm yr^{-1} up to 1000 m depth, and are a constant 0.08 cm yr^{-1} at depths greater than 1000 m (Yeager et al. 2004). However, pulsed deposition of sedimented oil near the Macondo wellhead was estimated to range from 3.8 to 5 cm thick (Joye et al. 2014), with the thickness of deposited material decreasing with distance from DWH (Ziervogel et al. 2016). Limiting the analysis to the upper 3 cm of sediment provides a conservative estimate of communities likely impacted by contaminant exposure and reduces the influence of natural seep hydrocarbons on our analysis, which can be present in deeper fractions of near-seep sediments. In addition, the 0–3 cm upper fraction of sediments contained 65 to 98% of the total abundance of macrofauna, and 77 to 93% of the total meiofauna, based on data from all cores.

Diversity among sampling locations was examined using Shannon diversity (H' [$\log_e$]) and Pielou's evenness (J') indices, and rarefaction based on untransformed abundance data using the DIVERSE function in PRIMER Statistical Software version 7 (Clarke et al. 2014). Colonial organisms (e.g. Porifera and Bryozoa) were excluded from diversity calculations (H', J') and multivariate community analysis. Variability within sampling locations was assessed for univariate measures of macrofaunal and meiofaunal density, diversity, and hydrocarbon concentrations by using the log/log relationship of the mean and standard deviation, each transformed as $\ln(x + 1)$ (Warwick & Clarke 1993). Variability among Bray-Curtis similarities within sampling locations was also assessed using relative multivariate dispersion (MVDISP). MVDISP values range from 0 to 2, with greater variability, and consequently higher MVDISP values, expected in impacted sediments (Warwick & Clarke 1993). Community structure was assessed by examining the overall contribution of higher-level taxa. Multivariate analysis of community structure across sampling locations was performed on square-root transformed macrofaunal data and fourth-root transformed meiofaunal data using Bray-Curtis similarities in PRIMER version 7 (Clarke et al. 2014). Macrofaunal and meiofaunal communities were analyzed separately. Community patterns were examined using non-metric multidimensional scaling (nMDS), cluster analysis, similarity of percentages (SIMPER), and 1-way permutational ANOVA (PERMANOVA; Anderson et al. 2008) with sampling location as the main factor.

To compare potential impacts from DWH at deep-sea coral habitats, principal component analysis (PCA) was used to examine the relationship among biological and environmental variables. PCA analysis was performed using only the measured environmental variables (depth, distance from DWH, Tox50, SatHC, aluminum, barium, copper, percent mud, and percent organic carbon) in order to reduce the data into contaminant axes (e.g. PC 1 and PC2). Distance, Tox50, SatHC, aluminum, barium, and copper were log-transformed using $\ln(x+1)$ and percent mud and percent organic carbon were logit-transformed for normality. After transformation, all variables were standardized to a common scale with a distribution mean of 0 and standard deviation of 1 using PRIMER 7 software. PC axes with eigenvalues >1 were compared to biological variables (macrofaunal and meiofaunal density, density variance, diversity, diversity variance, and MVDISP) using correlation analysis (Zar 1999), computed using the program R (R Development Core Team 2011). PC axes were also compared to the abundance of specific indicator taxa, including nematodes, harpacticoid copepods, amphipods, and the polychaete families Capitellidae, Cirratulidae, and Spionidae. Spearman rank correlation was used for correlation analyses.

To test whether specific environmental variables were responsible for observed patterns in the infaunal community assemblages, distance-based linear modeling (DistLM) was performed, with the resultant model visualized using distance-based redundancy analysis (dbRDA), using the PERMANOVA+ add on package to PRIMER 7 (Anderson et al. 2008). DistLM performs nominal tests of each variable's explanatory power on the multivariate community structure and builds a statistical model of the explanatory power of a suite of variables when considered together (Anderson et al. 2008). While PCA reduces multiple environmental variables into single descriptive variables which can be compared to univariate community metrics, DistLM allows for the incorporation of the full multivariate community data combined with environmental variables and is not constrained by the assumptions of normality implied in PCA. In addition, DistLM partitions the variation associated with each included variable, providing an estimate of the amount of variation in the data explained by each variable. For the DistLM procedure, data were reduced to mean values per sampling location. Variables included were depth, distance from DWH, barium, aluminum, copper, Tox50, SatHC, organic carbon, and mud content, transformed as above for the PCA. These variables were chosen due to their potential to structure and/or influence sediment communities. The DistLM analysis applied the corrected Akaike's information criterion (AICc), which was developed to handle situations where the ratio of samples to predictor variables is small. The most appropriate model, or 'best' model, is identified as the model with the lowest AICc value that explains the greatest amount of variation in the community data. The 'best' model was visualized using dbRDA, with the percent variation explained by the dbRDA axes compared to those of an unconstrained principal coordinate ordination (PCO) of the original Bray-Curtis similarity matrix of community composition. Models with similar AICc values (±1 unit) are generally considered to be probable alternative explanatory combinations (Anderson et al. 2008).

RESULTS

Environmental drivers

The highest concentrations of Tox50 and SatHC were observed at MC294A, with mean concentrations 2 to 4 times higher than at the next highest locations, MC344A, MC294B, and MC297C (Table 2,

Fig. 3a). Concentrations of SatHC were significantly negatively correlated with distance from the wellhead (ρ = −0.70, p = 0.007) (Fig. 3b). Elevated concentrations of copper, barium, and aluminum were measured at sites closest to DWH (MC294, MC297, MC344), while somewhat elevated concentrations of barium and aluminum were found at the more distant locations AT357B and MC036A, respectively (Table 2).

Macrofaunal and meiofaunal community patterns

The lowest and highest macrofaunal densities occurred at sites closest to the wellhead, ranging from 4739 ± 2385 individuals m^{-2} at MC294A to 24 961 ± 7067 individuals m^{-2} at MC297C (Table 3, Fig. 3c). Similar to macrofaunal densities, average meiofaunal densities were the lowest and highest at sites closest to the wellhead (Table 3, Fig. 3d), ranging from 1979 ± 341 individuals per 32 cm^2 at MC344A to 7242 ± 1524 individuals per 32 cm^2 at MC297C. Diversity results estimated by rarefaction (Fig. 4) indicated that MC294A, MC294B, MC297C, and MC507A had the lowest macrofaunal taxa richness, while MC344 and MC036 had the highest taxa richness. However, none of the rarefaction curves approached an asymptote, except when all samples were combined (regional diversity), suggesting adequate sampling of the regional species pool but undersampling at individual locations.

Multivariate analysis of infaunal communities indicated that macrofaunal and meiofaunal community composition differed among sampling locations (PERMANOVA, macrofauna: df = 12, pseudo-F = 2.63, p = 0.0001; meiofauna: df = 12, pseudo-F = 3.34, p = 0.0001; Fig. 5). nMDS analysis of macrofaunal community assemblages overlaid with corresponding sum Tox50 concentrations (Fig. 5a) indicated that sites with high concentrations of Tox50 were highly variable and most similar to one another. Cluster analysis (Fig. 5b) illustrated that infaunal community structure from sites closest to the wellhead (MC294, MC297, MC344) differed from those farther away (SIMPROF, p < 0.05). For meiofaunal communities, nMDS (Fig. 6a) and cluster analysis (Fig. 6b) indicated that MC344A and MC344B had significantly different communities from all other samples except one collected at MC297A. The higher similarity among meiofaunal communities (83 to 98%) may have been due to the lower taxonomic resolution of the meiofaunal community data compared to the macrofaunal communities.

Specific taxonomic composition of major groups (Fig. 3c,d) varied among sampling locations. For macrofaunal communities, MC294A and MC294B in particular had the highest proportion of polychaetes (>76%) while no other location had >67%. In contrast, AT357B had the lowest proportion of polychaetes (42%) and higher proportions of crustaceans (29%) and oligochaetes (9%) than at MC294. SIMPER analysis indicated that the polychaete families Paraonidae (32%), Sigalionidae (16%), Cirratulidae (15%), and Maldanidae (11%) contributed the most to the similarity among cores at MC294A and MC294B. The primary taxa responsible for dissimilarities between MC294 (A and B) and all the other

Table 2. Environmental variables from 0–3 cm sediments at sampling locations in the vicinity of the DWH oil spill. Tox50: sum of 53 polycyclic aromatic hydrocarbons (see Table A1 in the Appendix); SatHC: total saturated hydrocarbons; values for mud are percent grain size <63 µm. Numbers in parentheses correspond to ±1 SE

Location	Tox50 (ppb)		SatHC (ppb)		Aluminum (ppm)	Barium (ppm)	Mud (%)	Copper (ppm)	Organic carbon (%)	
MC297A	593	(36)	5981	(269)	14800	661	98.27	25.20	0.83	(0.00)
MC297B	642	(71)	5777	(1152)	15150	465	99.41	25.40	1.09	(0.10)
MC297C	1171	(242)	10076	(921)	15050	326	99.75	25.80	1.47	(0.11)
MC294A	5590	(3884)	20302	(9442)	14050	344	99.37	23.55	1.12	(0.09)
MC294B	1369	(1086)	8251	(5786)	17900	704	98.76	26.20	1.01	(0.15)
MC118B	359	(66)	2748	(482)	13000	381	82.67	17.60	0.79	(0.13)
MC344A	1501	(56)	3398	(331)	11295	362	96.24	20.80	0.91	(0.11)
MC344B	557	(12)	4398	(73)	15050	1419	99.20	29.85	0.96	(0.14)
MC203A	497	(50)	2221	(103)	14650	277	90.41	20.50	0.91	(0.11)
MC036A	578	(43)	2891	(106)	15650	384	98.18	21.30	0.93	(0.06)
MC036B	431	(17)	2676	(31)	14800	383	95.93	23.00	1.01	(0.12)
MC507A	420	(8)	1303	(16)	10750	351	99.50	15.60	0.81	(0.04)
AT357B	681	(5)	4825	(393)	9410	1735	80.95	21.30	0.74	(0.06)

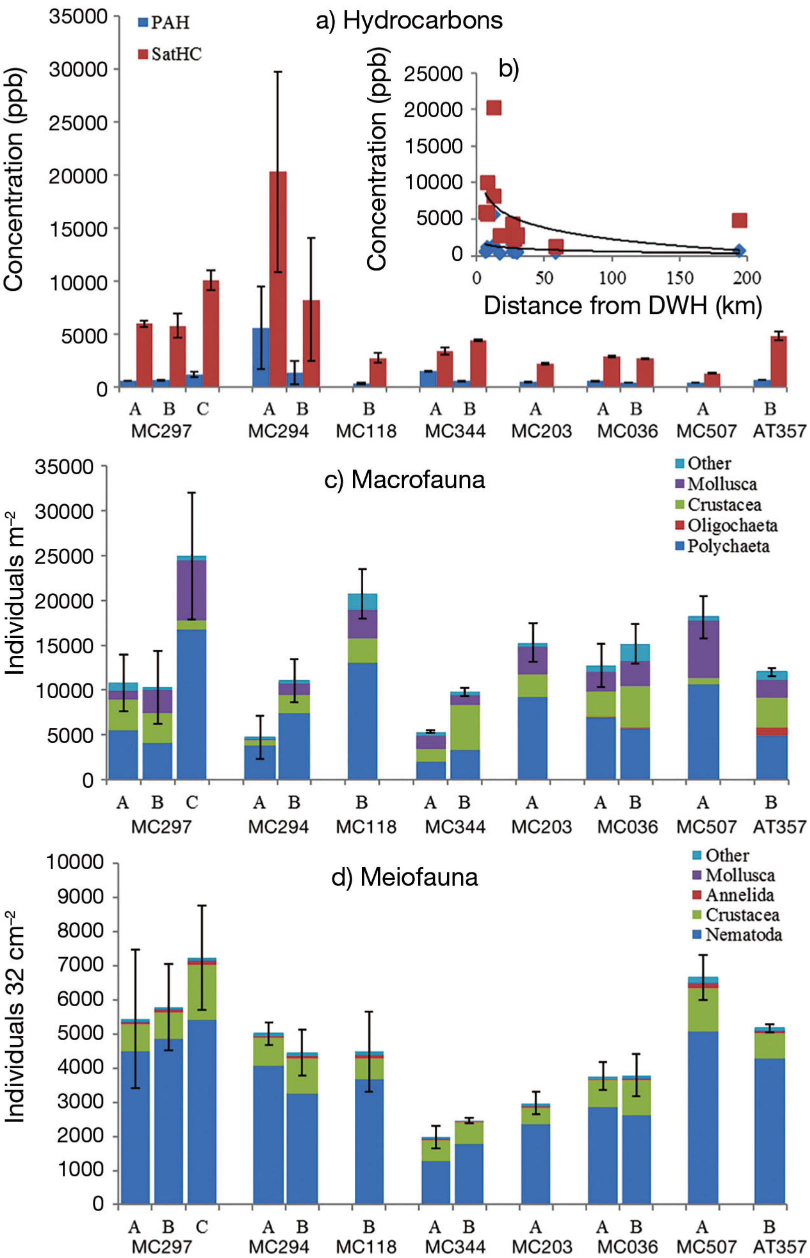

Fig. 3. (a) Hydrocarbon concentrations (ppb) in sediments at sample locations in the Gulf of Mexico following the DWH oil spill (see Fig. 1). PAH: sum of 53 polycyclic aromatic hydrocarbons; SatHC: total saturated hydrocarbons. (b) Relationship of hydrocarbon concentrations with distance from DWH (km). Spearman rank correlations for Tox50: $\rho = -0.39$, $p = 0.018$, $y = -352.8 \times \ln(x) + 2187.8$; for SatHC: $\rho = -0.70$, $p = 0.007$, $y = -2280 \times \ln(x) + 12745$. (c) Mean macrofaunal density (individuals m^{-2}) and composition. (d) Mean meiofaunal density (individuals per 32 cm^2) and composition. Error bars show ±1 SE

locations included Paraonidae (2 to 6%), Capitellidae (1 to 6%), Dorvilleidae (3 to 8%), Bivalvia (2 to 6%), Sigalionidae (1 to 3%), Cirratulidae (3 to 4%) and Maldanidae (3 to 5%). For meiofauna (Fig. 3d), nematodes were the dominant taxa (>69%), with the highest percentages occurring at MC297A, MC297B, MC294A, MC-118B, and AT357B. Meiofaunal crustacean composition ranged from 13 to 27%, with the lowest percent contributions at MC297A, MC297B, MC-118B, and AT357B.

Injury to coral-associated sediment benthos

PCA of only the environmental variables, including potential spill indicators, yielded 3 PC factors with eigenvalues >1, accounting for 81.0% of the variation in the data (Fig. 7). PC1 explained 49.4% of the variation in the data, and was positively loaded by distance from the DWH and negatively loaded by all other variables except barium. PC1 was identified as the primary contaminant axis, representing hydrocarbon concentrations, organic carbon content, mud content, copper concentrations, and distance from DWH. PC2 accounted for an additional 18.8% of the variation in the data and was primarily influenced by positive loading of barium, another contaminant indicator. PC3, not shown, explained an additional 12.8% of the data and was primarily positively loaded by distance, Tox50, and SatHC, and primarily negatively loaded by aluminum, barium, and copper.

Macrofaunal density was negatively correlated with PC2 ($\rho = -0.67$, $p = 0.012$), which was heavily influenced by barium so that density decreased as barium concentrations increased. Macrofaunal Shannon diversity (H' $\log_e$) was positively correlated with PC1 ($\rho = 0.73$, $p = 0.004$) so that diversity increased with distance from the DWH and lower contaminant concentrations. Variance in macrofaunal density was negatively correlated with PC1 ($\rho = -0.67$, $p = 0.012$) so that variance increased with increased concentrations of Tox50 and SatHC. While meiofaunal density and Shannon diversity were not correlated with any of the PC axes, variance

Table 3. Mean macrofaunal and meiofaunal community variables for 0–3 cm core depths at sampling locations in the vicinity of the DWH oil spill, showing macrofaunal density (individuals m^{-2}), meiofaunal density (individuals per 32 cm^2), Shannon diversity (H' $\log_e$), evenness (Pielou's J'), relative dispersion assessed using relative multivariate dispersion (MVDISP), and the nematode to copepod ratio for meiofauna (N:C). Numbers in parentheses correspond to ±1 SE

Location	Macrofauna				Meiofauna				
	Density	H' ($\log_e$)	J'	Relative dispersion	Density	H' ($\log_e$)	J'	N:C	Relative dispersion
MC297A	10821 (3153)	2.73 (0.15)	0.96 (0.01)	1.364	5450 (2022)	0.68 (0.08)	0.28 (0.03)	5.80 (1.25)	1.404
MC297B	10321 (4080)	2.25 (0.21)	0.90 (0.02)	1.659	5792 (1272)	0.62 (0.02)	0.25 (0.01)	7.46 (0.59)	1.368
MC297C	24961 (7067)	2.15 (0.19)	0.80 (0.04)	0.574	7242 (1524)	0.77 (0.02)	0.32 (0.02)	4.36 (0.63)	1.263
MC294A	4739 (2385)	1.78 (0.05)	0.94 (0.03)	1.659	5014 (340)	0.62 (0.03)	0.26 (0.01)	6.23 (0.91)	0.825
MC294B	11058 (2371)	2.31 (0.10)	0.90 (0.03)	0.651	4457 (683)	0.83 (0.01)	0.34 (0.01)	3.89 (0.11)	1.351
MC118B	20748 (2744)	2.89 (0.03)	0.92 (0.01)	0.326	4489 (1169)	0.69 (0.06)	0.27 (0.03)	6.76 (0.72)	0.719
MC344A	5371 (182)	2.32 (0.08)	0.93 (0.02)	1.473	1979 (341)	0.95 (0.06)	0.40 (0.01)	2.40 (0.29)	1.439
MC344B	9795 (483)	2.57 (0.04)	0.92 (0.02)	1.426	2469 (89)	0.81 (0.05)	0.34 (0.02)	3.49 (0.67)	0.684
MC203A	15271 (2161)	2.77 (0.01)	0.92 (0.00)	0.822	2974 (324)	0.71 (0.03)	0.31 (0.01)	5.88 (0.83)	0.614
MC036A	12744 (2422)	2.62 (0.13)	0.90 (0.01)	0.899	3770 (402)	0.74 (0.05)	0.32 (0.01)	4.48 (0.80)	0.93
MC036B	15166 (2212)	2.90 (0.05)	0.93 (0.02)	0.791	3793 (615)	0.89 (0.04)	0.36 (0.02)	2.87 (0.30)	1.035
MC507A	18115 (2374)	2.50 (0.15)	0.85 (0.04)	0.202	6653 (658)	0.73 (0.17)	0.31 (0.09)	5.82 (2.83)	1.474
AT357B	12006 (483)	2.65 (0.09)	0.92 (0.01)	0.791	5170 (128)	0.63 (0.05)	0.26 (0.02)	7.61 (0.92)	0.211

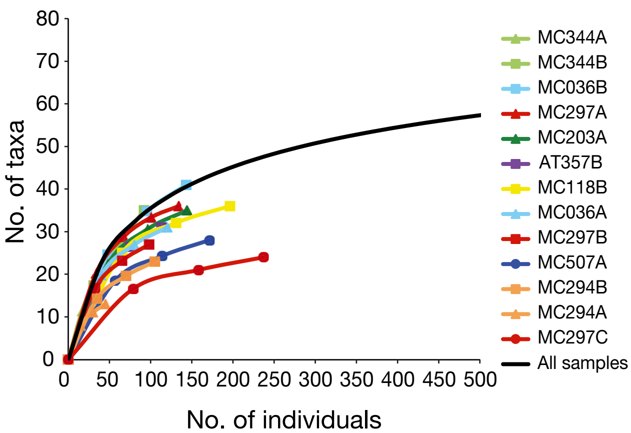

Fig. 4. Estimation of macrofaunal taxa richness in deep-sea sediments in the vicinity of the DWH oil spill, showing Coleman rarefaction curves by sampling location and for all samples combined (black curve)

in meiofaunal Shannon diversity was positively correlated with PC1 (ρ = 0.69, p = 0.0095), and increased with distance from the DWH and decreased contaminant concentrations. No other measures of community variability (i.e. macrofaunal Shannon diversity variance, meiofaunal density variance, or MVDISP) were significantly correlated with any PC axis.

In addition to the biological community metrics, the responses of specific pollution indicator taxa differed among the contaminant axes identified by the PCA. Abundances of Capitellidae and Cirratulidae were negatively correlated with PC2 (Capitellidae: ρ = –0.65, p = 0.015; Cirratulidae: ρ = –0.82, p = 0.0006). Capitellidae dominated the infaunal communities at MC297C, representing 47% of the polychaetes, while no other location had more than 7%. Spionidae were positively correlated with PC1 (ρ = 0.74, p = 0.004) with increased abundance associated with distance from DWH and decreased contaminant concentrations. Amphipod abundance was negatively correlated with PC3 (ρ = –0.65, p = 0.016), and increased with decreasing concentrations of hydrocarbons. Amphipods, known to be sensitive to contamination, were completely absent at MC294 where the highest Tox50 concentrations were measured (Table 2, Fig. 3a). In the meiofaunal communities, neither the N:C ratio or its variance were significantly correlated with any PC axis (p > 0.05). However, the sites with the highest hydrocarbon concentrations, MC294A, MC294B and MC297C, had an elevated ratio of copepod nauplii relative to other copepods (12 to 19), potentially a result of increased recruitment of nauplii at these sites, while all other sites except AT357B had ratios <9.

Multivariate community analysis of impact

Because the PCA approach was limited to the univariate biological data (macrofaunal and meiofaunal abundance, diversity, and N:C), interpretation of those results is not representative of the entire multivariate community. Of the 9 environmental variables analyzed, the DistLM marginal tests indicated that 3 variables independently contributed to a significant

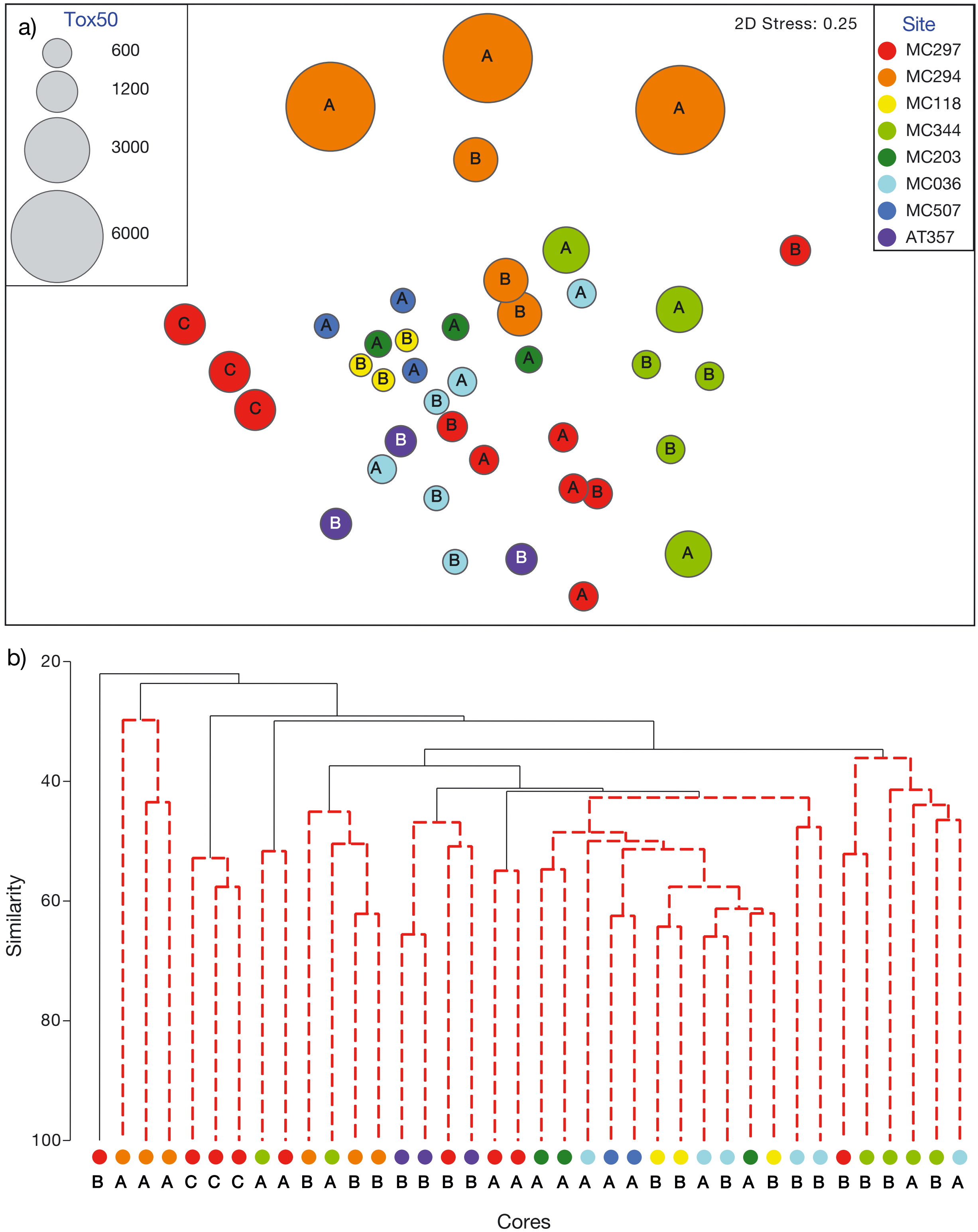

Fig. 5. (a) Non-metric multi-dimensional scaling (nMDS) plot of Bray-Curtis similarities among individual sediment cores (0–3 cm depth) sampled from areas in the vicinity of the DWH oil spill, based on square-root transformed density data of macrofauna with hydrocarbon concentration overlay. 2D stress = 0.25; this is a high stress value (>0.2), indicating that the complexity of the data is not presented well in a 2D plane. (b) Cluster diagram of Bray-Curtis similarities among individual sediment cores (0–3 cm) based on square-root transformed density data of macrofauna. Black lines connect clusters of samples that are significantly different from each other ($p < 0.05$)

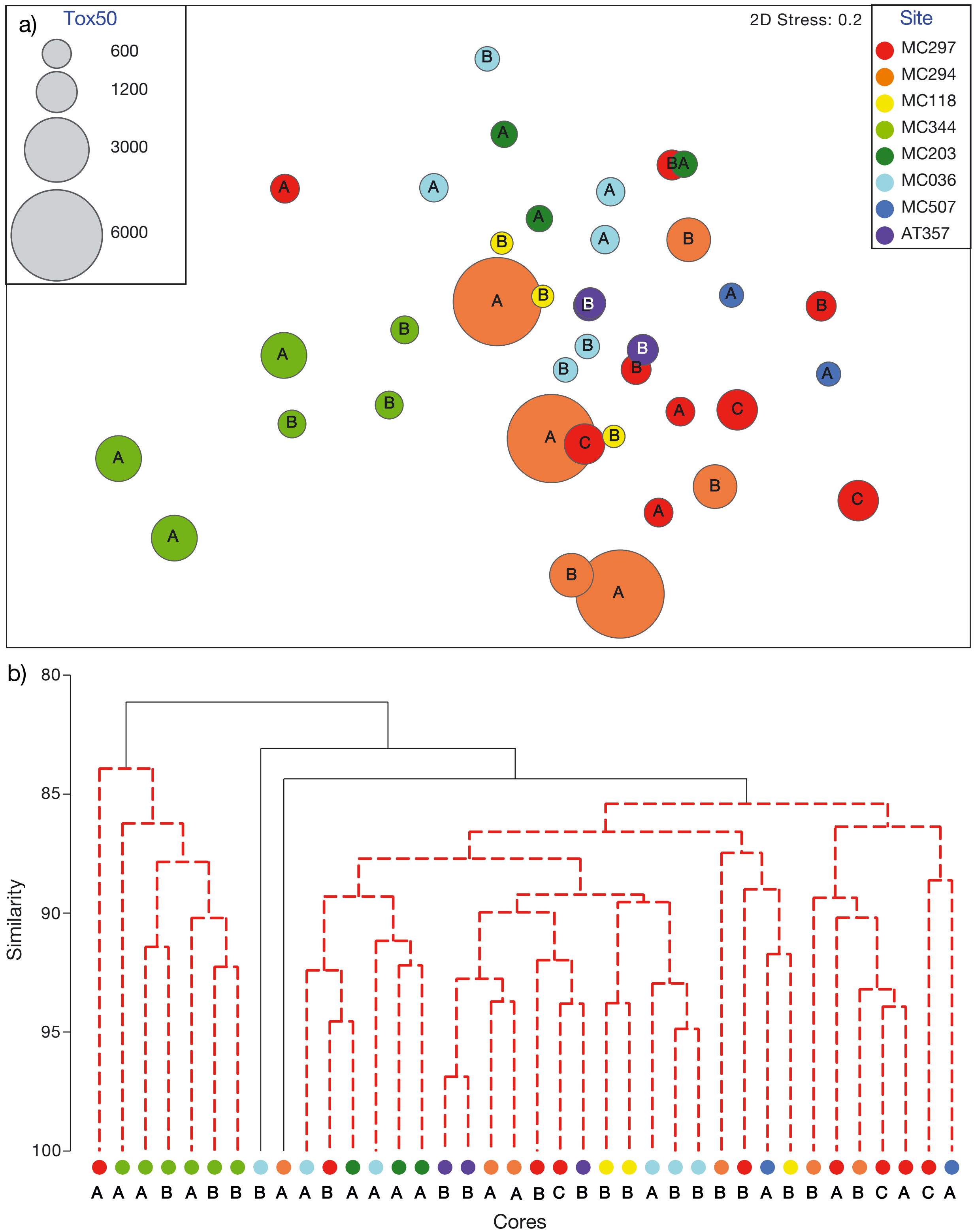

Fig. 6. (a) Non-metric multi-dimensional scaling (nMDS) plot and (b) cluster diagram of Bray-Curtis similarities among individual sediment cores (0–3 cm) sampled from areas in the vicinity of the DWH oil spill, based on fourth-root transformed density data of meiofauna with hydrocarbon concentration overlay. In (a), 2D stress = 0.2. In (b), black lines connect clusters of samples that are significantly different from each other ($p < 0.05$)

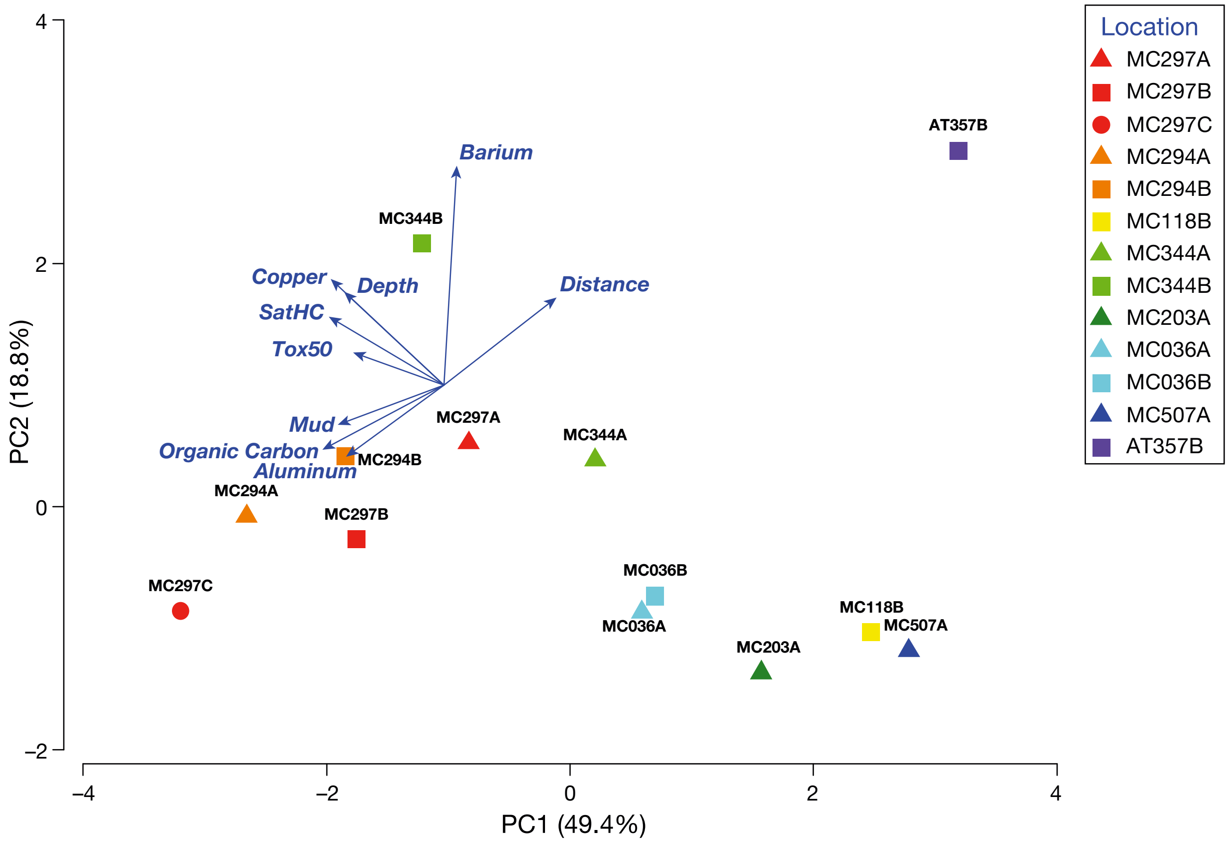

Fig. 7. Principal components analysis of environmental data for each sampling location in the vicinity of the DWH oil spill in the Gulf of Mexico

proportion of the variation (15.2 to 19.0%) in the macrofaunal communities (Table 4). Tox50 explained the highest proportion of the variation (19.0%), followed by depth (15.4%) and SatHC (15.3%) (Table 5). Although the full model (all variables) explained the most variability in macrofaunal communities (AICc = 199.55, 83.1%; Table 5), Tox50 was identified as providing the best overall solution for explaining the structure of the macrofaunal communities (AICc = 95.118; Table 5). This is further demonstrated by the dbRDA (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m561p051_supp.pdf)

Table 4. Results of distance-based linear modeling (DistLM) analysis of individual environmental variables for multivariate macrofaunal and meiofaunal communities for deep-sea sediments in the vicinity of the DWH oil spill. Tox50: sum of 53 polycyclic aromatic hydrocarbons (PAHs); SatHC: total saturated hydrocarbons; SS (trace): total sum of squares. Distance, Tox50, SatHC, aluminum, barium, and copper were log-transformed using ln(x+1) and percent mud and percent organic carbon were logit-transformed for normality. Values in **bold** indicate statistical significance ($p < 0.05$)

Variable	Macrofauna				Meiofauna			
	SS (trace)	Pseudo-*F*	p	R^2	SS (trace)	Pseudo-*F*	p	R^2
Depth	2499.0	2.01	**0.013**	0.154	257.4	3.60	**0.008**	0.246
Distance	1251.0	0.92	0.529	0.077	57.2	0.64	0.643	0.055
Tox50	3086.6	2.59	**0.001**	0.190	136.3	1.65	0.146	0.130
SatHC	2471.2	1.98	**0.016**	0.153	128.5	1.54	0.185	0.123
Aluminum	849.9	0.61	0.902	0.052	26.3	0.28	0.926	0.025
Barium	1777.0	1.35	0.156	0.110	26.6	0.29	0.925	0.026
Copper	1478.4	1.10	0.339	0.091	74.7	0.85	0.487	0.072
Mud	1329.7	0.98	0.464	0.082	57.9	0.65	0.654	0.055
Organic carbon	1380.2	1.02	0.405	0.085	44.1	0.49	0.780	0.042

Table 5. The best results from the DistLM analysis of macrofaunal and meiofaunal communities, based on corrected Akaike's information criterion (AICc). Values are presented in order of decreasing importance and include a model for all variables. Tox50: sum of 53 polycyclic aromatic hydrocarbons; SatHC: total saturated hydrocarbons; RSS: residual sum of squares

AICc	R^2	RSS	Variables
Macrofauna			
95.12	0.190	13117	Tox50
95.69	0.154	13705	Depth
95.71	0.153	13733	SatHC
96.12	0.330	10850	Depth, Tox50
96.36	0.110	14427	Barium
96.62	0.091	14726	Copper
96.68	0.301	11332	Depth, SatHC
96.71	0.085	14824	Organic carbon
96.74	0.298	11380	Tox50, barium
96.75	0.082	14874	Mud
199.55	0.831	3728	All variables
Meiofauna			
57.60	0.463	560.6	Depth, mud
58.54	0.246	786.9	Depth
59.53	0.554	465.9	Depth, SatHC, mud
59.84	0.543	477.2	Depth, PAH, mud
59.94	0.357	671.2	Depth, SatHC
60.40	0.130	908.0	Tox50
60.47	0.330	699.2	Depth, distance
60.51	0.123	915.8	SatHC
60.64	0.322	708.4	Depth, organic carbon
60.71	0.318	712.4	Depth, Tox50
162.02	0.854	152.7	All variables

of the best DistLM model (Tox50), which separates MC294A, MC294B, MC297C, and MC344A from the other sampling locations based on their high Tox50 content. The model visualized in the dbRDA (Fig. S1) accounts for all the fitted variation explained by Tox50 concentrations on a single axis. In comparison, the first axis of the PCO explained 23.9% of the total variation in the unconstrained community data. Variables with similar, but higher, AICc values (Table 5) included depth and SatHC, suggesting these are both potentially important factors influencing macrofaunal community structure. This analysis suggests that MC294, MC297, and MC344 are impacted sites based on Tox50 concentrations alone, and are consistent with our PCA results, where the contaminant axes PC1 and PC2 were negatively correlated with macrofaunal diversity and abundance.

Key environmental variables potentially influencing meiofaunal community structure were different from those identified in the macrofauna analysis. Depth was the only variable that independently explained a significant proportion of the variation (24.6%; Table 4). The best solution provided by the DistLM analysis was a combination of depth and mud content (AICc = 57.599) accounting for 46.3% of the variation within the multivariate community data, with most the variation explained by dbRDA Axis 1 (41.8%; Fig. S2 in the Supplement). An unconstrained PCO of the meiofaunal community data indicated that the first 2 PCO axes explained 72% of the variation. The large difference between the variation explained by the DistLM model (46.3%) and the unconstrained ordination (72%) suggests some variation in meiofaunal community data that cannot be attributed to the measured environmental variables. The second best solution was depth (AICc = 58.541; Table 5), suggesting environmental conditions unrelated to the oil spill also may be important in structuring meiofaunal communities.

DISCUSSION

Deep-sea coral-associated sediment communities located closest to the DWH wellhead exhibited high variability in meiofaunal and macrofaunal densities and hydrocarbon concentrations, although this was more pronounced for macrofaunal communities. Our results are consistent with Schmalhausen's law, which states that organisms exhibit greater variance in their life history traits when stressed (Lewontin & Levins 2000). Increased variability in benthic communities has been documented as a response to contamination from oil extracting activities in the North Sea (Gray et al. 1990), and is one of the indicators of oil spill impact near DWH. Consistent with our results for sediment communities, injury from the DWH spill to coral colonies was patchy both across sites and within individual coral colonies (Fisher et al. 2014b), suggesting heterogeneity in the dispersal and deposition of DWH-derived contaminants. Similarly, Valentine et al. (2014) demonstrated that deposition of hydrocarbons in the region around DWH was patchy based on analysis of surface hopane concentrations. Corals can modify hydrodynamic flows (Mienis et al. 2012), which likely affected the deposition of oil on the sediments surrounding the colonies. In particular, the additional substrate and hydrodynamic heterogeneity created by the coral colonies likely led to even more patchy deposition of the sedimented oil and may have also contributed to the high variability in ecological response documented in the nearby infaunal communities.

Injuries to sediment communities adjacent to corals described here are consistent with the extent of impact described by Fisher et al. (2014a,b) on actual coral colonies, including impacts detected at 3 of the 4 sites closest to the wellhead: MC294, MC297, and MC344. Although MC294 was not the closest site to DWH, it had the highest sediment SatHC and Tox50 concentrations, the lowest macrofaunal densities and diversity, and pollution-sensitive amphipods were absent. All of these factors indicate a biological response to toxins released during the oil spill. Sediments at MC297C had the second highest hydrocarbon concentrations coupled with the highest organic carbon concentrations, second-lowest diversity values (H'), low abundances of amphipods, high dominance of opportunistic capitellid polychaetes, and the highest macrofaunal densities recorded of all sampling locations. These patterns are consistent with a community shift and possibly adverse response to hydrocarbon concentrations and organic enrichment. Hydrocarbon concentrations were the third highest at MC297A and MC297B, and corresponded to low macrofaunal densities and high variability in macrofaunal and meiofaunal communities, suggesting moderate but patchy injuries from the spill-related hydrocarbon exposure. Finally, MC344 exhibited community patterns consistent with infaunal injury, with low densities of macrofauna corresponding to high surface hydrocarbon concentrations. Although MC344 had a higher diversity of taxa and higher proportion of crustaceans compared to MC294 and MC297, MC344 may also be directly influenced by natural hydrocarbon seepage and elevated concentrations of subsurface sediment hydrocarbons (Fisher et al. 2014a). Natural seeps are present at these 3 sites (MC294, MC297, MC344; Garcia-Pineda et al. 2016) and the coral colonies are often found attached to authigenic carbonates produced in seep environments. However, the overall contribution of seep-derived oil in this region is relatively small compared to the NW GOM (MacDonald et al. 2015). Because our sampling locations within MC344 were in close proximity to active seeps containing megafauna, the associated infaunal community may have been less sensitive to hydrocarbon exposure following the spill. Across all sites, densities of pollution-sensitive Amphipoda and more tolerant Spionidae and Cirratulidae declined with increased hydrocarbon concentrations, indicating concentrations of hydrocarbons reached toxic levels sufficient to adversely affect even the hardier macrofaunal taxa.

Although there was some evidence for increased variation in meiofaunal density at the sites near the DWH, meiofaunal community response did not uniformly exhibit the same patterns as the macrofaunal community. Meiofaunal communities in sediments adjacent to coral sites had similar ranges in density, diversity, and N:C ratios reported for those within the non-impacted soft-sediments (Montagna et al. 2013; 2016). In contrast to the results presented in Montagna et al. (2013), the N:C ratio was not positively correlated with the organic input associated with hydrocarbon contamination nor was it positively correlated with organic carbon content. In addition, the N:C values were close to mean values reported for pre-spill GOM soft sediments (5.7 ± 1.8; Baguley et al. 2006a). However, given that macrofaunal communities adjacent to corals differ from background soft-sediment habitats (Demopoulos et al. 2014, Fisher et al. 2014a), pre-spill coral-associated meiofaunal communities and their associated N:C ratios may also differ from what is known generally for the broader deep GOM. One potential factor for this difference in meiofaunal community response may have been the short generation times (i.e. turnover) and more rapid population growth exhibited in this size class of fauna. Samples in this study were collected 18 mo after the initiation of the spill. Given that meiofauna have high life-cycle turnover rates (Heip et al. 1982), they may have had sufficient time to recolonize sediments. Further, the initial impact response may have been masked by the population growth of some of the taxa. It is also possible that impacted meiofaunal communities were present at some of these sites but were not sampled in the cores due to the highly patchy distribution of contaminants. However, this study provides a post-spill baseline dataset of multiple meiofaunal parameters from which to track future changes and additional disturbance impacts.

The patterns observed in coral-associated sediment communities differed from those observed in 2010 for soft-sediment communities by Montagna et al. (2013). Increased contaminants, as described in the PCA (Fig. 7), were not correlated with the N:C ratio, a metric for meiofaunal response, but more directly related to decreased macrofaunal diversity and abundance. These results suggest that the infaunal community may continue to change over time following the spill. Macrofaunal densities from coral-associated sediments collected in 2011 (this study) were within the same range as those found in soft-sediment environments collected in the same year (Montagna et al. 2016). Taken together, research by Montagna et al. (2013, 2016), Baguley et al. (2015) and Fisher et al. (2014a) suggest the hydrocarbon-exposed benthic communities continued to shift in response to the spill through 2011. Specifically, organic enrichment from the spill would have resulted in a rapid response by meiofaunal organisms, the most readily available fauna to make use of the nutrients stemming from post-spill enhanced bacterial production (Baguley et al. 2015). A rapid response by meiofauna is consistent with the high N:C and meiofaunal abundance documented for soft-sediment communities and in coral-associated sediments at MC294 in 2010 (Montagna et al. 2013, Fisher et al. 2014a). Temporal changes in the infaunal communities occurred between 2010 and 2011 at MC294 (Fisher et al. 2014a), corresponding to high, but decreasing, surface sediment hydrocarbon concentrations. At MC294, macrofaunal and meiofaunal densities declined between 2010 and 2011, the opportunistic polychaete families Capitellidae, Cirratulidae, and seep-associated Dorvilleidae dominated the macrofaunal communities in 2010 but declined in 2011, and the N:C ratio decreased for meiofaunal communities. Data presented here indicate that although the macrofaunal community still exhibited signs of disturbance in 2011, the meiofaunal community may have already begun to recover from the event, similar to what was reported for temporal changes (2010 to 2011) in soft sediment environments (Montagna et al. 2016).

Additional multivariate analysis conducted in this study (DistLM) provided further insight into which contaminant and natural environmental variables were important in structuring macrofaunal and meiofaunal communities post-spill. Tox50 concentrations were strongly associated with macrofaunal community impact, consistent with Montagna et al. (2013). Tox50 was identified as the single variable most responsible for the observed variation in macrofaunal community structure, which included shifts in the abundance of specific taxa and their presence/absence among locations. The combination of depth with Tox50 concentrations explained 33% of the variation in macrofaunal communities, suggesting a synergistic effect of the 2 community structuring variables.

The presence of hydrocarbon seeps may be an additional factor contributing to variation within and among our sampling locations. However, we limited our analyses to the top 3 cm of sediment to isolate the sediment communities affected by recent deposition of oil and reduce the potential influence of subsurface hydrocarbon seepage. Multiple sites sampled are near natural seep environments, as indicated by surface oil slick image analysis (MacDonald et al. 2015, Garcia-Pineda et al. 2016) and the presence of hydrocarbon concentrations in deeper sediments (Fisher et al. 2014a). In Montagna et al. (2013), the PC3 axis was correlated with proximity to seeps, primarily structured by natural mud and aluminum content. However, the seep location data used in their analyses were based on acoustic seabed anomalies, which could include both active and inactive seeps. We are not aware of any baseline data for seep-specific infauna from this region in the GOM, so were unable to compare observed impacted and non-impacted communities to seep communities. Increased resolution of seep environment mapping and additional sampling of seep sediment communities in areas within and outside the impact zones would therefore further our understanding of how these communities respond to pulsed hydrocarbon inputs.

Of the sites with perturbed sediment infaunal communities identified in our study (MC294, MC297, and MC344), only MC294 is spatially located in an area suggested by Montagna et al. (2013) to be 'moderately' impacted, while both MC297 and MC344 were in the unimpacted areas. Although analysis of additional sites included in Baguley et al. (2015) extended the spatial area of impact proposed by Montagna et al. (2013), our impacted sites still fall outside the area of impact for soft-sediment communities. As suggested by Fisher et al. (2014a), the sampling pattern of Montagna et al. (2013) and Baguley et al. (2015) lacked many samples in the SE direction from the DWH wellhead, where MC297 and MC344 are located, thus their interpretation of resource injury toward the SE may be incomplete. The contamination footprint map based on hopane concentrations in sediment (Valentine et al. 2014) encompasses our MC297 and MC118 sampling locations. Individual samples with elevated hopane levels were also found at MC344 (Valentine et al. 2014), which is again indicative of the patchy deposition of Macondo oil. The dispersant DOSS (dioctyl sodium sulfosuccinate) was detected in surface sediments at MC297 and MC344, providing further evidence that the effects of the spill reached these locations (White et al. 2014). Finally, the amended impact map suggested by Fisher et al. (2014b) for coral communities is corroborated by our sediment results, with impacts detected at MC294, MC297, and MC344.

Using multivariate analyses, we differentiated the infauna associated with coral habitats at injured sites from those that were uninjured based on differences in macrofaunal communities and surface sediment hydrocarbon concentrations. This study presents the first detailed description of the relationship between post-spill deep-sea coral-associated sediment meioand macrofaunal communities and their sediment environment, providing essential baseline information for these communities. By tracking changes in infaunal community structure and identifying their potential for recovery, information gathered in this study can be used to inform monitoring of the natural recovery of these habitats as well as infaunal community response following future catastrophic oil-spill pollution events.

Acknowledgements. NOAA's Office of Response and Restoration provided funding for this research as part of the NRDA for the DWH oil spill. Additional funding was provided to A.W.J.D. from the USGS OCS Environments program. This manuscript was subject to internal review, and the authors thank Rob Ricker (NOAA), Christopher Lewis (IEc), Gwendolyn McCarthy (NOAA), the crew of the *Holiday Chouest*, Chuck Fisher and his lab. Additionally, special thanks go out to J. McClain-Counts, J. Frometa, W. Jenkins, and the rest of the USGS Benthic Ecology Group for assistance at sea, sample sorting, and thoughtful discussions during the preparation of this manuscript. We also thank 3 anonymous reviewers for their insightful comments. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

Anderson M, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth

Ansari ZA, Ingole B (2002) Effect of an oil spill from MV *Sea Transporter* on intertidal meiofauna at Goa, India. Mar Pollut Bull 44:396–402

Baguley JG, Montagna PA, Hyde LJ, Kalke RD, Rowe GT (2006a) Metazoan meiofauna abundance in relation to environmental variables in the northern Gulf of Mexico deep sea. Deep-Sea Res I 53:1344–1362

Baguley JG, Montagna PA, Lee W, Hyde LJ, Rowe GT (2006b) Spatial and bathymetric trends in Harpacticoida (Copepoda) community structure in the northern Gulf of Mexico deep-sea. J Exp Mar Biol Ecol 330:327–341

Baguley JG, Montagna PA, Hyde LJ, Rowe GT (2008) Metazoan meiofauna biomass, grazing, and weight-dependent respiration in the northern Gulf of Mexico deep sea. Deep-Sea Res II 55:2607–2616

Baguley JG, Montagna PA, Cooksey C, Hyland JL and others (2015) Community response of deep-sea soft-sediment metazoan meiofauna to the Deepwater Horizon blowout and oil spill. Mar Ecol Prog Ser 528:127–140

Bang HW, Lee W, Kwak IS (2009) Detecting points as developmental delay based on the life-history development and urosome deformity of the harpacticoid copepod, *Tigriopus japonicus sensu lato*, following exposure to benzo(a)pyrene. Chemosphere 76:1435–1439

Bejarano AC, Chandler GT, He L, Coull BC (2006) Individual to population level effects of South Louisiana crude oil water accommodated hydrocarbon fraction (WAF) on a marine meiobenthic copepod. J Exp Mar Biol Ecol 332: 49–59

Bourque JR, Robertson CM, Brooke S, Demopoulos AWJ (2016) Macrofaunal communities associated with chemosynthetic habitats from the US Atlantic margin: a comparison among depth and habitat types. Deep-Sea Res II, doi:10.1016/j.dsr2.2016.04.012

Burgess R (2001) An improved protocol for separating meiofauna from sediments using colloidal silica sols. Mar Ecol Prog Ser 214:161–165

Camilli R, Reddy CM, Yoerger DR, Van Mooy BAS and others (2010) Tracking hydrocarbon plume transport and biodegradation at Deepwater Horizon. Science 330: 201–204

Carman KR, Todaro MA (1996) Influence of polycyclic aromatic hydrocarbons on the meiobenthic-copepod community of a Louisiana salt marsh. J Exp Mar Biol Ecol 198:37–54

Carr RS, Chapman DC, Presley BJ, Biedenbach JM and others (1996) Sediment porewater toxicity assessment studies in the vicinity of offshore oil and gas production platforms in the Gulf of Mexico. Can J Fish Aquat Sci 53: 2618–2628

Carvalho R, Wei CL, Rowe G, Schulze A (2013) Complex depth-related patterns in taxonomic and functional diversity of polychaetes in the Gulf of Mexico. Deep-Sea Res I 80:66–77

Chanton J, Zhao T, Rosenheim BE, Joye S and others (2015) Using natural abundance radiocarbon to trace the flux of petrocarbon to the seafloor following the Deepwater Horizon oil spill. Environ Sci Technol 49:847–854

Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2014) Change in marine communities: an approach to statistical analysis and interpretation, 3rd edn. PRIMER-E, Plymouth

Coull B, Hicks G, Wells J (1981) Nematode/copepod ratios for monitoring pollution: a rebuttal. Mar Pollut Bull 12: 378–381

Danovaro R, Gambi C, Dell'Anno A, Corinaidesi C and others (2008) Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr Biol 18:1–8

Dean HK (2008) The use of polychaetes (Annelida) as indicator species of marine pollution: a review. Int J Trop Biol 56:11–38

Demopoulos AWJ, Bourque JR, Frometa J (2014) Biodiversity and community composition of sediment macrofauna associated with deep-sea *Lophelia pertusa* habitats in the Gulf of Mexico. Deep-Sea Res I 93:91–103

Doughty CL, Quattrini AM, Cordes EE (2014) Insights into the population dynamics of the deep-sea coral genus *Paramuricea* in the Gulf of Mexico. Deep-Sea Res II 99: 71–82

Fisher CR, Demopoulos AWJ, Cordes EE, Baums IB, White HK, Bourque JR (2014a) Coral communities as indicators of ecosystem-level impacts of the Deepwater Horizon spill. Bioscience 64:796–807

Fisher CR, Hsing PY, Kaiser C, Yoerger D and others (2014b) Footprint of Deepwater Horizon blowout impact to deep-water coral communities. Proc Natl Acad Sci USA 111: 11744–11749

Fleeger JW, Chandler GT (1983) Meiofauna responses to an experimental oil spill in a Louisiana salt marsh. Mar Ecol Prog Ser 11:257–264

Folk RL (1968) Petrology of sediment rocks. Hemphill, Austin, TX

Gage JD, Tyler PA (1991) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge

Garcia-Pineda O, MacDonald I, Silva M, Shedd W, Daneghar Asl S, Schumaker B (2016) Transience and persistence of natural hydrocarbon seepage in Mississippi Canyon, Gulf of Mexico. Deep-Sea Res II 129:119–129

Gesteira JLG, Dauvin JC (2000) Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. Mar Pollut Bull 40:1017–1027

Giere O (1979) The impact of oil pollution on intertidal meiofauna. Field studies after the La Coruna-spill, May 1976. Cah Biol Mar 20:231–251

Girard F, Fu B, Fisher CR (2016) Mutualistic symbiosis with ophiuroids limited the impact of the Deepwater Horizon oil spill on deep-sea octocorals. Mar Ecol Prog Ser 549: 89–98

Gomez Gesteira JL, Dauvin JC, Salvande Fraga M (2003) Taxonomic level for assessing oil spill effects on soft-bottom sublittoral benthic communities. Mar Pollut Bull 46:562–572

Grant A, Briggs AD (2002) Toxicity of sediments from around a North Sea oil platform: Are metals or hydrocarbons responsible for ecological impacts? Mar Environ Res 53:95–116

Gray JS, Elliott M (2009) Ecology of marine sediments: from science to management. Oxford University Press, Oxford

Gray JS, Waldichuk M, Newton AJ, Berry RJ, Holden AV, Pearson TH (1979) Pollution-induced changes in populations [and discussion]. Philos Trans R Soc B Biol Sci 286: 545–561

Gray JS, Clarke KR, Warwick RM, Hobbs G (1990) Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. Mar Ecol Prog Ser 66:285–299

Haedrich RL, Devine JA, Kendall VJ (2008) Predictors of species richness in the deep-benthic fauna of the northern Gulf of Mexico. Deep-Sea Res II 55:2650–2656

Heip CHR, Vincx M, Smol N, Vranken G (1982) The systematics and ecology of free-living marine nematodes. Helminthological Abstracts B Plant Nematology 51:1–31

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol Annu Rev 23:399–489

Ho KT, McKinney RA, Kuhn A, Pelletier MC, Burgess RM (1997) Identification of acute toxicants in New Bedford harbor sediments. Environ Toxicol Chem 16:551–558

Hsing PY, Fu B, Larcom EA, Berlet SP and others (2013) Evidence of lasting impact of the Deepwater Horizon oil spill on a deep Gulf of Mexico coral community. Elementa 1: 000012

Joye SB, Teske AP, Kostka JE (2014) Microbial dynamics following the Macondo oil well blowout across Gulf of Mexico environments. Bioscience 64:766–777

Lambshead PJD (1984) The nematode/copepod ratio some anomalous results from the Firth of Clyde. Mar Pollut Bull 15:256–259

Lewontin R, Levins R (2000) Schmalhausen's Law. Capitalism Nat Socialism 11:103–108

MacDonald IR, Reilly JF Jr, Best SE, Venkataramaiah R, Sassen R, Guinasso NL Jr, Amos J (1996) Remote sensing inventory of active oil seeps and chemosynthetic communities in the northern Gulf of Mexico. In: Schumacher D, Abrams MA (eds) Hydrocarbon migration and its near-surface expression: AAPG Memoir 66:27–37

MacDonald IR, Leifer I, Sassen R, Stine P, Mitchell R, Guinasso N (2002) Transfer of hydrocarbons from natural seeps to the water column and atmosphere. Geofluids 2: 95–107

MacDonald IR, Garcia-Pineda O, Beet A, Daneshgar Asl S and others (2015) Natural and unnatural oil slicks in the Gulf of Mexico. J Geophys Res Oceans 120:8364–8380

Mienis F, de Stigter HC, White M, Duineveld G, de Haas H, van Weering TCE (2007) Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. Deep-Sea Res I 54:1655–1674

Mienis F, van der Land C, de Stigter HC, van de Vorstenbosch M, de Haas H, Richter T, van Weering TCE (2009) Sediment accumulation on a cold-water carbonate mound at the Southwest Rockall Trough margin. Mar Geol 265:40–50

Mienis F, Duineveld GCA, Davies AJ, Ross SW, Seim H, Bane J, van Weering TCE (2012) The influence of near-bed hydrodynamic conditions on cold-water corals in the Viosca Knoll area, Gulf of Mexico. Deep-Sea Res I 60: 32–45

Montagna PA, Harper DE Jr (1996) Benthic infaunal long-term response to offshore production platforms in the Gulf of Mexico. Can J Fish Aquat Sci 53:2567–2588

Montagna PA, Li J (1997) Modelling contaminant effects on deposit feeding nematodes near Gulf of Mexico production platforms. Ecol Modell 98:151–192

Montagna PA, Baguley JG, Cooksey C, Hartwell I and others (2013) Deep-sea benthic footprint of the Deepwater Horizon blowout. PLOS ONE 8:e70540

Montagna PA, Baguley JG, Cooksey C, Hyland JL (2016) Persistent impacts to the deep soft-bottom benthos one year after the Deepwater Horizon event. Integr Environ Assess Manag, doi:10.1002/ieam.1791

Pearson TR, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution in the marine environment. Oceanogr Mar Biol Annu Rev 16: 229–311

Pequegnat WE, Gallaway BJ, Pequegnat LH (1990) Aspects of the ecology of the deep-water fauna of the Gulf of Mexico. Am Zool 30:45–64

Peterson CH, Anderson SS, Cherr GN, Ambrose RF and others (2012) A tale of two spills: novel science and policy implications of an emerging new oil spill model. Bioscience 62:461–469

Qu F, Nunnally CC, Lemanski JR, Wade TL, Amon RMW, Rowe GT (2015) Polychaete annelid (segmented worms) abundance and species composition in the proximity (6–9 km) of the Deepwater Horizon (DWH) oil spill in the deep Gulf of Mexico. Deep-Sea Res II 129:130–136

Quattrini AM, Etnoyer PJ, Doughty C, English L and others (2014) A phylogenetic approach to octocoral community structure in the deep Gulf of Mexico. Deep-Sea Res II 99: 92–102

R Development Core Team (2011) R: a language an environment for statistical computing. R Foundation for Statistical Computing, Vienna

Raffaelli DG (1987) The behaviour of the nematode/copepod ratio in organic pollution studies. Mar Environ Res 23: 135–152

Rowe GT, Kennicutt MC II (eds) (2009) Northern Gulf of Mexico continental slope habitats and benthic ecology study: final report. US Dept. of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA

Rowe GT, Polloni PT, Horner SG (1974) Benthic biomass estimates from the northwestern Atlantic Ocean and the northern Gulf of Mexico. Deep-Sea Res 21:641–650

Thurber AR, Sweetman AK, Narayanaswamy BE, Jones DOB, Ingels J, Hansman RL (2014) Ecosystem function and services provided by the deep sea. Biogeosciences 11:3941–3963

USA v. BP et al. (United States of America v. BP Exploration & Production Inc. et al.) (2015) Findings of fact and conclusions of law: Phase Two trial. In re: Oil spill by the oil rig 'Deepwater Horizon' in the Gulf of Mexico, on April 20, 2010, No. MDL 2179, 2015 WL 225421 (LA. E.D. Jan. 15, 2015). (Doc. 14021). U.S. District Court for the Eastern District of Louisiana

Valentine DL, Fisher GB, Bagby SC, Nelson RK, Reddy CM, Sylva SP, Woo MA (2014) Fallout plume of submerged oil from Deepwater Horizon. Proc Natl Acad Sci USA 111: 15906–15911

Veiga P, Besteiro C, Rubal M (2010) Meiofauna communities in exposed sandy beaches on the Galician coast (NW Spain), six months after the Prestige oil spill: the role of polycyclic aromatic hydrocarbons (PAHs). Sci Mar 74: 385–394

Wade TL, Soliman Y, Sweet ST, Wolff GA, Presley BJ (2008) Trace elements and polycyclic aromatic hydrocarbons (PAHs) concentrations in deep Gulf of Mexico sediments. Deep-Sea Res II 55:2585–2593

Warwick RM (1981) The nematode/copepod ratio and its use in pollution ecology. Mar Pollut Bull 12:329–333

Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. J Exp Mar Biol Ecol 172:215–226

Wei CL, Rowe GT, Fain Hubbard G, Scheltema AH and others (2010) Bathymetric zonation of deep-sea macrofauna in relation to export of surface phytoplankton production. Mar Ecol Prog Ser 399:1–14

Wei CL, Rowe GT, Escobar-Briones E, Nunnally C, Soliman Y, Ellis N (2012) Standing stocks and body size of deep-sea macrofauna: predicting the baseline of 2010 Deepwater Horizon oil spill in the northern Gulf of Mexico. Deep-Sea Res I 69:82–99

Weston DP (1990) Quantitative examination of macrobenthic community changes along an organic enrichment gradient. Mar Ecol Prog Ser 61:233–244

White HK, Hsing PY, Cho W, Shank TM and others (2012) Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. Proc Natl Acad Sci USA 109:20303–20308

White HK, Lyons SL, Harrison SJ, Findley DM, Liu Y, Kujawinski EB (2014) Long-term persistence of dispersants following the Deepwater Horizon oil spill. Environ Sci Technol Lett 1:295–299

Yeager KM, Santschi PH, Rowe GT (2004) Sediment accumulation and radionuclide inventories (^{239,240}Pu, ^{210}Pb and ^{234}Th) in the northern Gulf of Mexico, as influenced by organic matter and macrofaunal density. Mar Chem 91:1–14

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ

Ziervogel K, Joye SB, Arnosti C (2016) Microbial enzymatic activity and secondary production in sediments affected by the sedimentation pulse following the Deepwater Horizon oil spill. Deep-Sea Res II 129: 241–248

Appendix. Table A1. List of polycyclic aromatic hydrocarbons (PAHs) and saturated hydrocarbons used to calculate Tox50. Due to co-elutions, the number of compounds listed for a sum may be less than or greater than the number specified (e.g. PAH 44 may contain 45 compounds). Benzo(k)fluoranthene is reported as co-eluting with benzo(j)fluoranthene by some laboratories, while benzo(j)fluoranthene is never reported independently. Thus either benzo(k)fluoranthene or benzo(j+k)fluoranthene will be reported, but not both. Similarly for benzo(b)fluoranthene and benzo(b+j)fluoranthene and for dibenzo(a,h+a,c)-anthracene and dibenzo(a,h)anthracene. Chrysene is reported as co-eluting with triphenylene

Tox50 ChemName		
Acenaphthene	C1-Naphthobenzothiophenes	C4-Fluoranthenes/pyrenes
Acenaphthylene	C1-Phenanthrenes/anthracenes	C4-Naphthalenes
Anthracene	C2-Chrysenes	C4-Naphthobenzothiophenes
Benzo(a)anthracene	C2-Dibenzothiophenes	C4-Phenanthrenes/anthracenes
Benzo(a)fluoranthene	C2-Fluoranthenes/pyrenes	Chrysene + Triphenylene
Benzo(a)pyrene	C2-Fluorenes	Chrysene
Benzo(b)fluoranthene	C2-Naphthalenes	Dibenzo(a,h)anthracene
Benzo(b+j)fluoranthene	C2-Naphthobenzothiophenes	Dibenzo(a,h+a,c)anthracene
Benzo(b)fluorene	C2-Phenanthrenes/anthracenes	Dibenzofuran
Benzo(e)pyrene	C3-Chrysenes	Dibenzothiophene
Benzo(g,h,i)perylene	C3-Dibenzothiophenes	Fluoranthene
Benzo(j+k)fluoranthene	C3-Fluoranthenes/pyrenes	Fluorene
Benzo(k)fluoranthene	C3-Fluorenes	Indeno(1,2,3-c,d)pyrene
Biphenyl	C3-Naphthalenes	Naphthalene
C1-Chrysenes	C3-Naphthobenzothiophenes	Naphthobenzothiophene
C1-Dibenzothiophenes	C3-Phenanthrenes/anthracenes	Phenanthrene
C1-Fluorenes	C4-Chrysenes	Pyrene
C1-Naphthalenes	C4-Dibenzothiophenes	

Editorial responsibility: Paul Snelgrove, St. John's, Newfoundland and Labrador, Canada

Submitted: March 2, 2016; Accepted: September 23, 2016
Proofs received from author(s): November 6, 2016