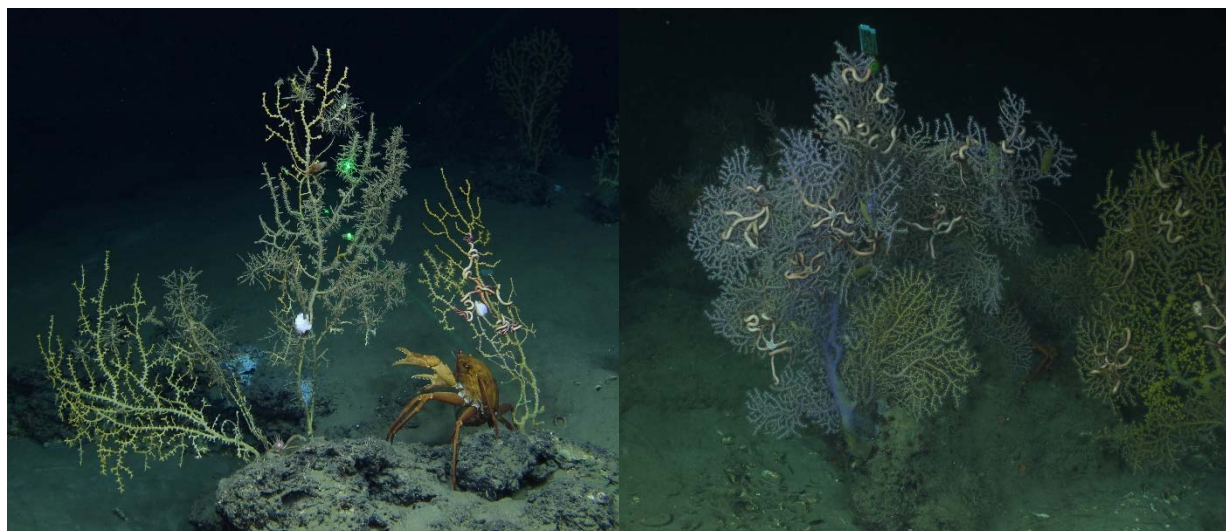


Quantifying Changes to Infaunal Communities Associated with Several Deep-Sea Coral Habitats in the Gulf of Mexico and Their Potential Recovery from the *Deepwater Horizon* Oil Spill



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ABOUT THE COVER

Left: Impacted coral at MC294. Right: Non-impacted coral at MC203. Photo credits: Oceaneering *Millennium* ROV, 2011.

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List of Abbreviations and Acronyms

AICc	Akaike Information Criterion for small sample sizes
ANOSIM	analysis of similarities
ANOVA	analysis of variance
BOEM	Bureau of Ocean Energy Management
dbRDA	distance-based redundancy analysis
DISTLM	distance-based linear modeling
DGOMB	deep Gulf of Mexico benthos
Gulf	Gulf of Mexico
HOV	human-occupied vehicle
HSD	honest squares difference
POC	particulate organic carbon
ROV	remotely-operated vehicle
SIMPER	similarity of percentages

1 Introduction

1.1 Background

1.1.1 Deep Gulf of Mexico and Deep-Sea Corals

Extensive information is available about infaunal soft-sediment communities in the Gulf of Mexico (Gulf) (Pequegnat et al. 1990, Rowe and Kennicutt II 2009, Wei et al. 2010), particularly from the large-scale sampling effort of the Deep Gulf of Mexico Benthos (DGOMB) project in the early 2000s (Rowe and Kennicutt II 2009). Infaunal soft-sediment communities in the northern Gulf differ by geographic location and depth (Rowe and Kennicutt II 2009, Wei et al. 2010). Density decreases with depth, while taxa diversity exhibits a mid-depth (1,100-1,300 m) maximum (Rowe and Kennicutt II 2009). Community composition is influenced by both geographic location and depth, with zones (as defined by Wei et al. 2010) encompassing specific depth ranges, ranging from 635 to 3,314 m, and separated into east and west components. These zones were correlated to detrital particulate organic carbon (POC) export flux, primarily from the Mississippi River (Wei et al. 2010), where POC flux decreases with depth (Biggs et al. 2008). The flux of POC has also been found to be higher in the northeast Gulf than the northwest (Biggs et al. 2008), and consequently, biomass of infaunal communities is positively correlated with sediment organic carbon content (Morse and Beazley 2008).

Most of the deep Gulf is composed of soft-sediment environments, but the relative flat seafloor is punctuated in areas with other heterogeneous habitats, including chemosynthetic environments and deep-sea coral habitats. Deep-sea corals create a complex three-dimensional structure that enhances local biodiversity, supporting diverse and abundant fish and invertebrate communities (Mortensen et al. 1995, Costello et al. 2005, Henry and Roberts 2007, Ross and Quattrini 2007, Buhl-Mortensen et al. 2010). In recent years, knowledge of the sphere of influence of deep-sea corals has expanded, with evidence that coral habitats also influence surrounding sediments (Mienis et al. 2012, Demopoulos et al. 2014, Fisher et al. 2014, Demopoulos et al. 2016, Bourque and Demopoulos 2018). Deep-sea corals are capable of altering their associated biotic and abiotic environment, thus serving as ecosystem engineers (e.g., Jones et al. 1994). The depositional environment and associated hydrodynamic regime around coral habitats differ from the extensive expanses of soft-sediments that dominate the sea floor (e.g., Mienis et al. 2009a, 2009b, Mienis et al. 2009b, Mienis et al. 2012), with the three-dimensional structure of the coral causing turbulent flows that enhance sediment accumulation adjacent to coral structures. In the northern Gulf, deep-sea corals generally occur on mounds of authigenic carbonate (Schroeder 2002) where elevation above the benthic boundary layer into higher velocity laminar flows allows for increased availability of food resources (Buhl-Mortensen and Mortensen 2005). The different hydrodynamics around corals likely affects the sediment geochemistry and in turn infaunal community structure and function (Demopoulos et al. 2014).

Ecosystem-based research on Gulf infaunal communities has primarily focused on soft-sediment environments. Initial research on deep-sea coral-associated infaunal communities focused on *Lophelia pertusa* (e.g., Demopoulos et al. 2014), and more recent studies focused on octocorals (Fisher et al. 2014, Demopoulos et al. 2016, Bourque and Demopoulos 2018) and comparisons among coral habitat types (Bourque and Demopoulos 2018). Coral-adjacent sediment communities are distinctly different from nearby background soft-sediment (Demopoulos et al. 2014, Bourque and Demopoulos 2018), with a sphere of influence estimated to be between 14 and 100 m (Demopoulos et al. 2014, Bourque and Demopoulos 2018). The coral type (e.g., *L. pertusa*, *Madrepora oculata*, octocorals) also influences

sediment communities, with *L. pertusa* habitats distinct from both *M. oculata* and octocoral habitats (Bourque and Demopoulos 2018). Differences among coral communities are influenced by depth, location, and sediment organic content (Bourque and Demopoulos 2018), and the reef size and the amount of habitat complexity are potential factors (Demopoulos et al. 2014, Bourque and Demopoulos 2018). Fisher et al. (2014) also demonstrated that infaunal communities adjacent to individual colonies and multiple mixed species of octocorals also differ from infauna in northern Gulf non-coral soft sediments (Rowe and Kennicutt II 2009, Wei et al. 2010). Patterns in coral-associated communities are decoupled from the general depth relationships established for soft-sediment habitats in the Gulf (Wei et al. 2010), exhibiting a mid-depth (~800 m) maximum in density and no relationship with diversity (Bourque and Demopoulos 2018). These differences suggest additional local-scale processes (e.g., near-bottom currents affecting grain size, food availability, and larval dispersal) are driving infaunal community patterns across the Gulf region as a whole (Wei et al. 2010). Complex hydrodynamic environments around deep-sea corals may substantially alter sediment organic matter deposition (Mienis et al. 2009, Mienis et al. 2009, Mienis et al. 2012) and the typical depth/diversity relationship may be decoupled as a result of patchiness in sediment organic carbon content around deep-sea corals.

1.1.2 The *Deepwater Horizon* Oil Spill and Effects on Deep Sea Benthos

In April 2010, a blowout occurred at the *Deepwater Horizon* Macondo well site at 1,525 m depth, releasing approximately 3.19×10^6 barrels (134 million gallons; 507 million liters) of oil into the northern Gulf until it was capped in July 2010 (USA v. BP et al. 2015). Oil was present as surface sheens and a deep-water plume (Camilli et al. 2010) that deposited over a large area of the seafloor (Valentine et al. 2014, Chanton et al. 2015). The release of the dispersant Corexit® further dispersed oil into the hydrographically-stratified water column, limiting transport into surface waters and retaining oil particles at depth (Camilli et al. 2010, Valentine et al. 2014, White et al. 2014).

The spill impacts were widespread, but it was unclear how the deep-sea benthic communities were affected. Characterization of the sediment macrofaunal communities (>300 μm) is a well-established approach to tracking changes to impacted coastal and deep-sea communities worldwide (Gray et al. 1990, Hyland et al. 1999, Dean 2008, Manoukian et al. 2010). Sediment macrofauna are important components of benthic biodiversity, providing essential ecosystem functions, including transfer of energy, sediment bioturbation and stabilization, and organic matter decomposition (Gage and Tyler 1991, Danovaro et al. 2008, Gray and Elliott 2009, Thurber et al. 2014). They represent important indicators of oil-spill disturbance primarily due to their sedentary lifestyle, relatively rapid response to change, and sensitivity to ecological disturbances such as hydrocarbon contamination and organic enrichment (Pearson and Rosenberg 1978, Gray et al. 1979, Gray et al. 1990, Montagna and Harper Jr. 1996). Specific taxa are frequently used as pollution indicators, including the polychaete families Capitellidae, Cirratulidae, and Spionidae, which can rapidly colonize substrates and have a high tolerance to oil exposure (Gesteira et al. 2003, Dean 2008) and Amphipoda (Crustacea), which are sensitive to oil exposure (Gesteira and Dauvin 2000, Grant and Briggs 2002). By examining these communities and monitoring them over time, we can estimate the magnitude of impact and their ability to recover following disturbance.

Initial impacts from the *Deepwater Horizon* oil spill have been observed in both soft-sediment and coral-associated macrofaunal communities (Montagna et al. 2013, Fisher et al. 2014, Demopoulos et al. 2016, Montagna et al. 2016, Qu et al. 2016). The spatial extent of impact to soft-sediment infauna was estimated to be 172 km² in an area (Montagna et al. 2013) that corresponded to the estimated shape and extent of the deep-water plume (Camilli et al. 2010). High and moderate impacts were documented within 3 to 17 km from the wellhead, with communities exhibiting decreased macrofaunal and meiofaunal diversity corresponding to high concentrations of hydrocarbons and barium (Montagna et al. 2013). Impacts to

coral-associated sediments were documented at three sites (MC297, MC294, MC344) all within 22 km of the wellhead (Fisher et al. 2014, Demopoulos et al. 2016). Impacts were site specific; high hydrocarbon concentrations were associated with low macrofaunal density and diversity similar to a toxicity event (MC294), and high macrofaunal density and low diversity similar to an organic enrichment event (MC297), and high variability within all communities.

Temporal change in impacted deep-sea communities has been assessed over short time frames (one year) in soft-sediment (Montagna et al. 2016) and coral habitats (Fisher et al. 2014) and in reference to historical data (Qu et al. 2016). Overall declines in macrofaunal abundance and diversity of polychaete assemblages were documented near the wellhead (Qu et al. 2016), as compared to historical data (Rowe and Kennicutt II 2009, Wei et al. 2010, Carvalho et al. 2013). Between 2010 and 2011, Montagna et al. (2016) observed continued depression of macrofaunal diversity and taxa richness, but an increase in macrofaunal density in impacted zones, as compared to non-impacted areas with similar hydrocarbon concentrations in the sediments. Overall, Montagna et al. (2016) estimated that recovery of impacted deep-sea sediments would be on the scale of decades or longer. In contrast, Fisher et al. (2014) documented a reduction in hydrocarbon concentrations, albeit still higher than background sediments, at a single impacted coral site (MC294) between 2010 and 2011, with a decrease in macrofaunal density. The post-spill temporal studies (Fisher et al. 2014, Montagna et al. 2016) used comparable collection methods in both years, but collection methods of historical samples differed in the use of box cores (Rowe and Kennicutt II 2009, Wei et al. 2010, Carvalho et al. 2013), which are known to underestimate macrofaunal densities (Montagna et al. 2017). Use of consistent methods across studies or normalization of data from disparate methods is also important considerations for quantitatively assessing temporal change in the deep sea.

Though these multi-year studies have produced important baseline data, we lack information about the long-term impact of the *Deepwater Horizon* oil spill on benthic infaunal communities, particularly for impacted and injured deep-sea coral habitats, which are necessary for impact assessments, informing the development of future restoration plans and delineation of protected areas, and guiding long-term monitoring programs of deep-sea environments. Monitoring benthic infaunal communities will yield important insights into the patterns and trajectory of change within these ecosystems by identifying their sensitivity and resiliency to disturbance. As industry moves into deeper water, questions remain about impacts to deep-sea ecosystems. Therefore, it is imperative that monitoring efforts effectively identify and differentiate impacts from oil and gas activities from other forms of disturbance, including hurricanes and climate change.

1.2 Objectives

The primary objective was to document temporal change in deep-sea coral sediment community structure in order to track long-term responses to anthropogenic disturbance as compared to natural variability. Specifically, we assessed changes in benthic infaunal communities following the *Deepwater Horizon* oil spill at several deep-sea coral sites located in proximity to the well head and at reference, non-impacted sites between 2010 and 2016. To provide the appropriate context for assessing temporal change in post-spill communities, we assessed the potential differences between sediment communities associated with different coral habitats (e.g., octocorals, *L. pertusa*, *M. oculata*), as well as pre- and post-spill time-series samples at sites not within the vicinity of the oil spill. Last, pre- and post-spill coral-associated communities were compared to additional Gulf deep-sea habitats, including chemosynthetic seeps, shipwrecks, and soft-sediments that represent current baseline conditions in the deep Gulf from which to establish long-term monitoring studies.

2 Methods

2.1 Study Locations

Between 2010 and 2016, sediments were collected adjacent to deep-sea coral habitats at three impacted sites and two non-impacted sites in the northern Gulf (Figure 1; Table A-1). Detailed information on the site discovery, selection, and impact designation can be found in White et al. (2012), Fisher et al. (2014), and Demopoulos et al. (2016). Previous studies of deep-sea sediments in the Gulf were assessed in reference to impacted sites (Table A-1), including additional reference, non-impacted deep-sea coral habitats (263–1,095 m; Demopoulos et al. 2014, Demopoulos et al. 2016, Bourque and Demopoulos 2018), three chemosynthetic seep sites (1,400–2,384 m; Brooks et al. 2014), seven shipwreck sites (532–2,270 m; Demopoulos et al. 2017), and 45 soft-sediment communities from DGOMB (213–3,528 m; Rowe and Kennicutt II 2009). Site names correspond to Bureau of Ocean Energy Management (BOEM) Lease Block designations. Three types of reference coral habitats were included in analyses based on the dominant coral type at a given location: *L. pertusa* (Lophelia), *M. oculata* (Madrepora), and octocoral (Octocoral), where the primary octocoral taxa was either a single or mixed species of *Paramuricea*, *Callogorgia*, *Paragorgia* and/or *Chrysogorgia*.

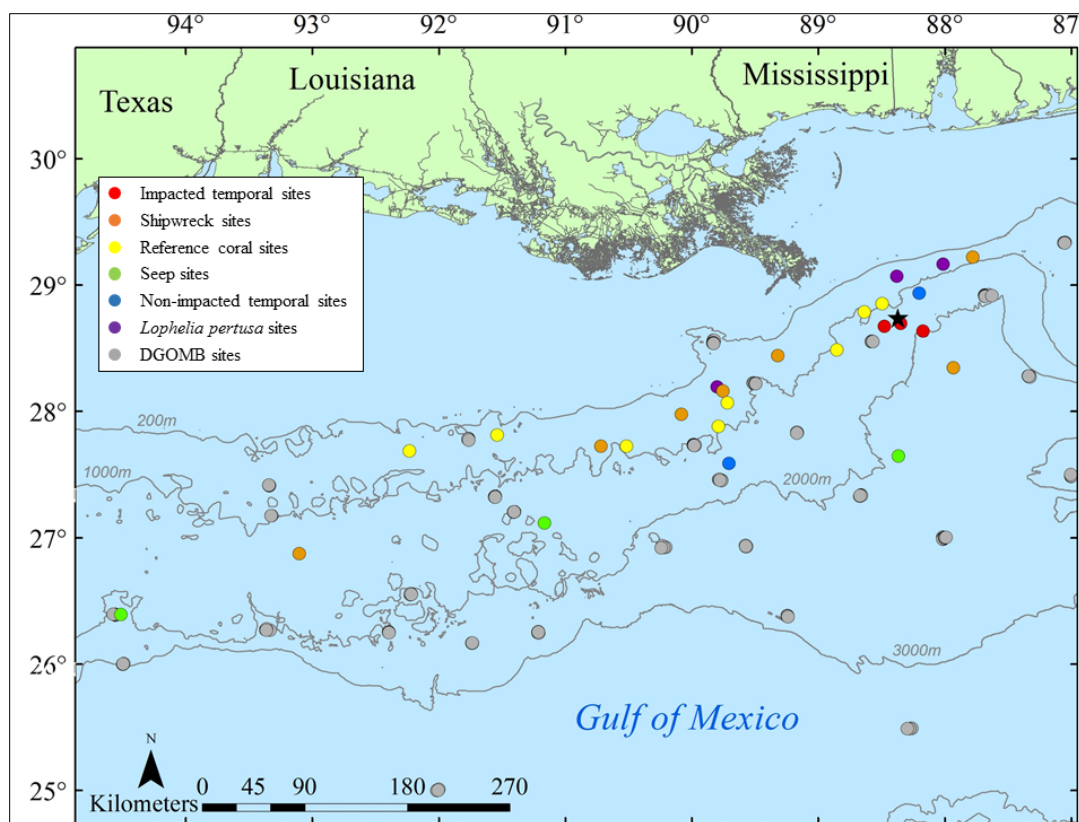


Figure 1. Map of study locations in the Gulf of Mexico

Different colored circles represent sampling locations at impacted sites (Fisher et al. 2014, Demopoulos et al. 2016), non-impacted reference sites (Demopoulos et al. 2016, Bourque and Demopoulos 2018), other deep-sea coral reference sites (Bourque and Demopoulos 2018), *Lophelia pertusa* sites (Demopoulos et al. 2014), chemosynthetic seep habitats (Brooks et al. 2014), shipwrecks (Demopoulos et al. 2017), and soft-sediments (Rowe and Kennicutt II 2009). The black star represents the site of the *Deepwater Horizon* oil spill at MC252.

2.2 Sample Collection and Processing

Sediment samples were collected between 2010 and 2016 on seven cruises in the Gulf (Table A-1). Push cores (6.35 cm diameter) were collected adjacent to coral habitats (within 1 m) using a remotely-operated vehicle (ROV) or a human-occupied vehicle (HOV). After recovery, all sediment cores were sectioned vertically (either 0–1, 1–3, 3–5, 5–10 cm or 0–2, 2–5, 5–10 cm). Data for impacted and non-impacted octocoral sites in 2011 were published in Demopoulos et al. (2016) and Fisher et al. (2014) (see Appendix 1). Data for cores collected at AT357 2013–2014 were published in Bourque and Demopoulos (2018). Temporal dynamics of sediment communities pre- and post-spill were assessed at one octocoral site– (GB299) and two *L. pertusa* sites (VK906 and VK826), with data published in Bourque and Demopoulos (2018). Sediment core sections processed for infauna analysis were preserved whole in an 8–10% buffered formalin solution until they were returned to the laboratory where they were stained with rose bengal and washed through a 300- μ m sieve to retain the macrofauna. Macrofauna were sorted with a dissecting microscope and identified to the lowest practical taxonomic level, including family level for polychaetes, peracarid crustaceans, and aplacophorans. Surface sediment sections (0–1 and 0–2 cm) from cores for geochemistry analysis were frozen whole at -20°C until they were returned to the lab. Grain size analysis was performed using the Folk method (Folk 1974). Sediment subsamples were homogenized prior to drying at $50\text{--}60^{\circ}\text{C}$ and acidified with 1.0 N phosphoric acid before weighing into tin boats. These samples were analyzed for organic carbon content and stable carbon isotope composition referenced to Vienna PeeDee Belemnite. Analyses were conducted at Washington State University using a Costech (Valencia, USA) elemental analyzer interfaced with a GV Instruments (Manchester, UK) IsoPrimeTM isotope ratio mass spectrometer.

2.3 Data Analysis

To assess the natural variability in coral sediment communities pre- and post-spill, infaunal communities at one octocoral site and two *L. pertusa* sites were investigated. Temporal dynamics of infaunal community parameters were assessed at three impacted sites, MC297, MC294, and MC344, and two non-impacted reference sites, MC036 and AT357. Macrofaunal density and univariate measures of biodiversity among years sampled were analyzed using one-way analysis of variance (ANOVA) followed by post-hoc test Tukey's Honest Squares Difference (HSD) for multiple comparisons. All data were tested for normality and heteroscedasticity using Shapiro-Wilk and Levene's test (Zar 1999) and \log_e -transformed when necessary. If transformation did not achieve normality or heteroscedasticity, a non-parametric Kruskal-Wallis test was used on univariate measures followed by a pairwise Wilcoxon test with a Holm correction for multiple comparisons. A significance level of $p < 0.05$ was used in all tests. Univariate statistics were computed with the program R (R Development Core Team 2016). Diversity was examined using the Shannon-Wiener diversity index ($H' \log_e$) and taxa evenness (Pielou's J'), based on untransformed abundance data using DIVERSE in PRIMER Statistical Software version 7 (Clarke and Gorley 2015).

Community structure was assessed by examining the overall contribution of higher level taxa, including Polychaeta, Oligochaeta, Crustacea, Mollusca, and other taxa. Other taxa included Halacaridae, Callipallenidae, Cnidaria (Anthozoa, Hydrozoa), Echinodermata (Holothuroidea, Ophiuroidea), Nemertea, Urochordata, Chaetognatha, Sipuncula, Echiura, and Turbellaria. Colonial taxa (i.e., Porifera, Bryozoa, Octocorallia) were not included in abundance, diversity, and community analyses but were included in overall taxa numbers. Multivariate analysis of community structure across cores was performed on square-root transformed abundance data using Bray-Curtis similarities in PRIMER version 7 (Clarke and Gorley 2015). Differences were examined using one-way and two-way analysis of similarity (ANOSIM). Similarity of percentages (SIMPER) was used to identify the taxa responsible for

discriminating between communities and to assess the variability within communities. A subset of the multivariate communities at impacted and non-impacted sites were assessed in conjunction with geographic location (latitude, longitude), sample year, bathymetric position (depth), sediment grain size (mud content), sediment organic carbon content, and stable carbon isotope composition ($\delta^{13}\text{C}$) using distance-based linear modelling (DISTLM) and distance-based redundancy analysis (dbRDA) using the PERMANOVA+ add on package to PRIMER 7 (Anderson et al. 2008) for locations where all of these data were available. DISTLM performs nominal tests of each variable's explanatory power on community structure and builds a multivariate statistical model of explanatory power of a suite of variables when considered together to determine the “best” model based on the Akaike information criterion for small sample sizes (AICc).

3 Results

3.1 Pre- and Post-Spill Communities

3.1.1 Octocoral Habitats

Only one octocoral site, GB299, was sampled both pre- and post-spill in 2009 and 2010. Macrofaunal density was similar between 2009 and 2010 (Table 1; One-way ANOVA, $F_{1,11}=1.39$, $p=0.26$), as was Shannon diversity (Table 1; One-way ANOVA, $F_{1,11}=0.90$, $p=0.36$) and taxa evenness (Table 1; One-way ANOVA, $F_{1,11}=0.00$, $p=0.99$). There was also no significant difference in community structure between 2009 and 2010 (Figure 2, Figure 3; One-way ANOSIM, $R=0.007$, $p=0.48$), with both years dominated by polychaetes (63-68%).

Table 1. Density and Diversity at Sites Sampled Both Pre- and Post-Spill

Octocoral sites includes GB299; *L. pertusa* sites include VK906 and VK826. Number in parentheses indicates one standard error.

Habitat	Octocoral		<i>Lophelia pertusa</i>	
	2009	2010	2009	2011
N	5	8	16	10
Density (individuals m ⁻²)	9,163 (727)	8,017 (617)	23,479 (1,851)	21,485 (1,075)
Shannon Diversity (H' _e)	2.50 (0.04)	2.39 (0.09)	2.47 (0.09)	2.74 (0.08)
Taxa Evenness (J')	0.92 (0.01)	0.92 (0.02)	0.84 (0.02)	0.87 (0.01)

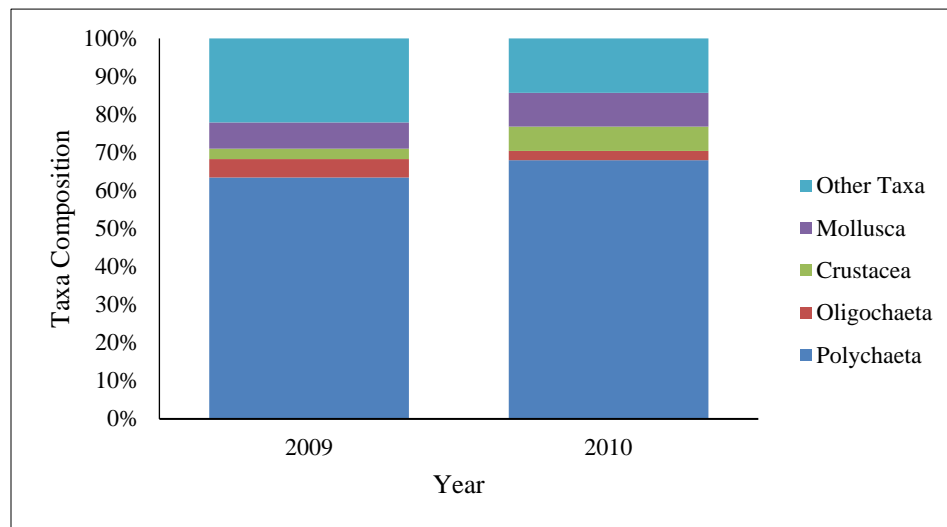


Figure 2. Percent taxonomic composition of macrofaunal abundance of octocoral communities at GB299 in 2009 and 2010.

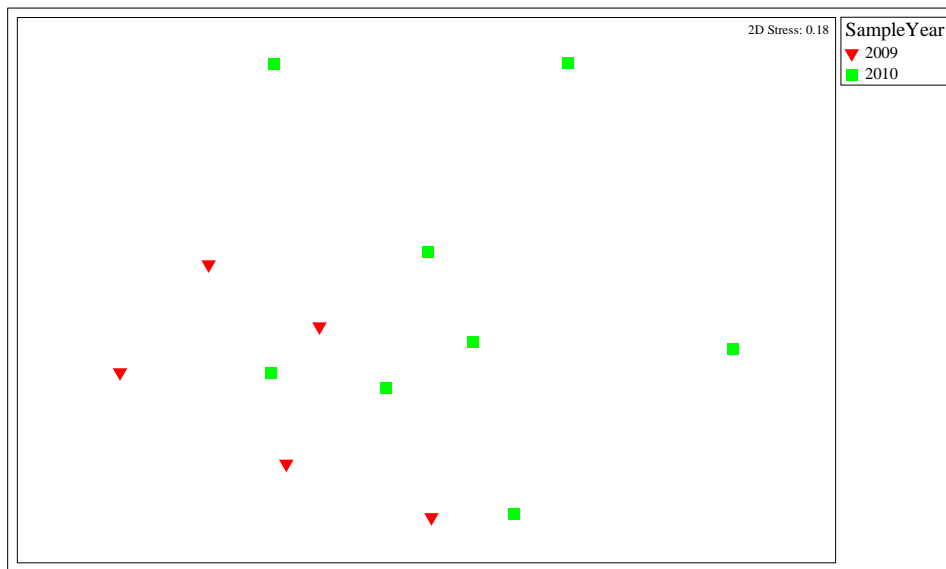


Figure 3. Non-metric multidimensional scaling of octocoral communities at GB299 collected in 2009 and 2010.

Based on Bray-Curtis similarities of square-root transformed abundance data.

3.1.2 *Lophelia pertusa* Habitats

Two *L. pertusa* sites were sampled pre-spill in 2009 and post-spill in 2011. Macrofaunal densities were similar between 2009 and 2011 (Table 1; One-way ANOVA, $F_{1,24}=0.63$, $p=0.43$) as was taxa evenness (Table 1; One-way ANOVA, $F_{1,24}=2.72$, $p=0.11$). Shannon diversity was significantly higher in 2011 than in 2009 (Table 1; One-way ANOVA, $F_{1,24}=4.41$, $p=0.046$). *Lophelia pertusa* communities were also significantly different between 2009 and 2011 (Figure 4, Figure 5; One-way ANOSIM, $R=0.13$, $p=0.041$), with differences due to higher densities of the polychaetes Oweniidae and Maldanidae in 2009, but higher densities of Gastropoda (Mollusca) and Oligochaeta in 2011 (17.3% of dissimilarity).

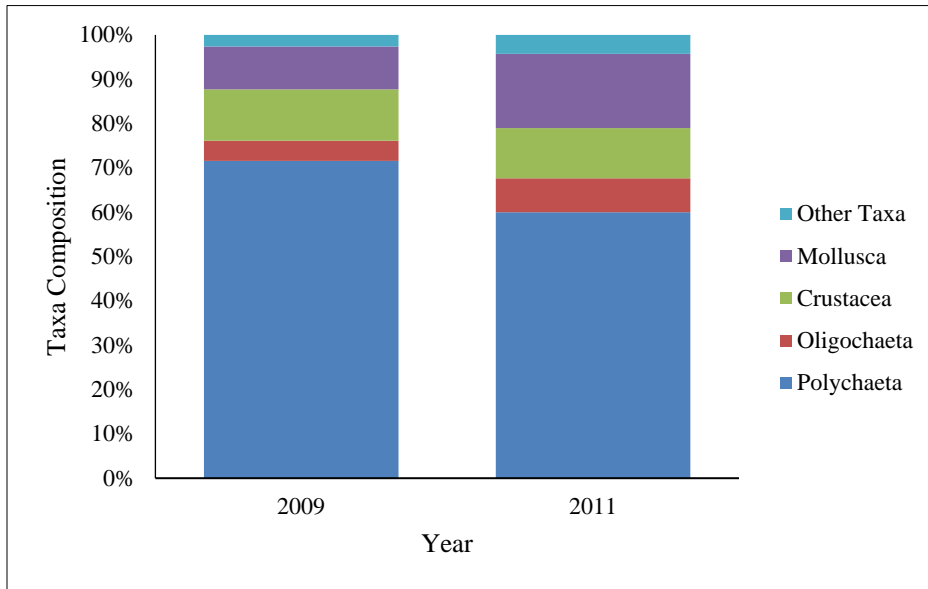


Figure 4. Percent taxonomic composition of macrofaunal abundance of *Lophelia pertusa* communities at VK906 and VK826 in 2009 and 2011.

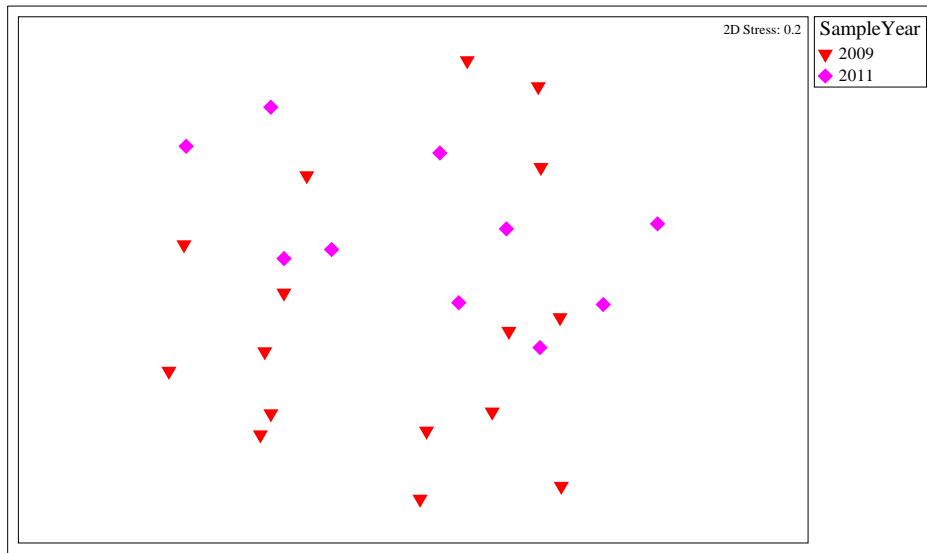


Figure 5. Non-metric multidimensional scaling of *Lophelia pertusa* communities at VK906 and VK826 in 2009 and 2011.

Based on Bray-Curtis similarities of square-root transformed abundance data.

3.2 Post-Spill Temporal Change in Non-Impacted Communities

There was no significant correlation of macrofaunal density and sample year at the non-impacted sites (Spearman correlation, $\rho=0.037$, $p=0.83$). Mean macrofaunal density was highest in 2015 (Figure 6; $18,062 \pm 5,963$ individuals m^{-2}) and lowest in 2014 ($6,973 \pm 1,691$ individuals m^{-2}); however, there was no significant difference among years (One-way ANOVA, $F_{4,31}=2.23$, $p=0.088$).

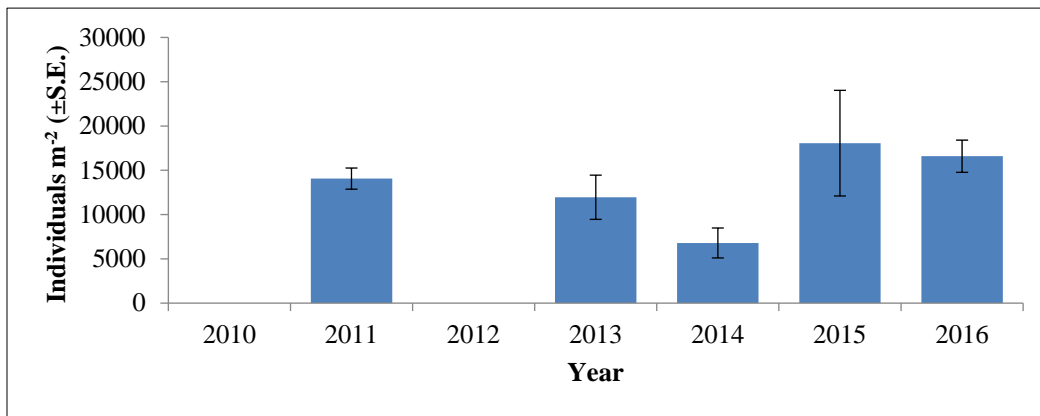


Figure 6. Macrofaunal density at non-impacted sites post-spill.

Error bars represent one standard error.

There was a significant correlation of Shannon diversity and sample year (Figure 7; Spearman correlation, $\rho=-0.55$, $p=0.0006$) with Shannon diversity decreasing with time. Shannon diversity varied among years at non-impacted sites (Figure 7; One-way ANOVA, $F_{4,31}=4.73$, $p=0.004$) with 2011 significantly higher than 2015 (Tukey HSD, $p=0.003$), while all other pairwise comparisons were non-significant. In contrast, there was no correlation of taxa evenness with sample year (Spearman correlation, $\rho=-0.32$, $p=0.061$), but evenness varied between years (Figure 8; Kruskal test, $\chi^2=11.73$, $p=0.019$), with taxa evenness significantly higher in 2011 than 2016 (Wilcoxon test, $p=0.047$).

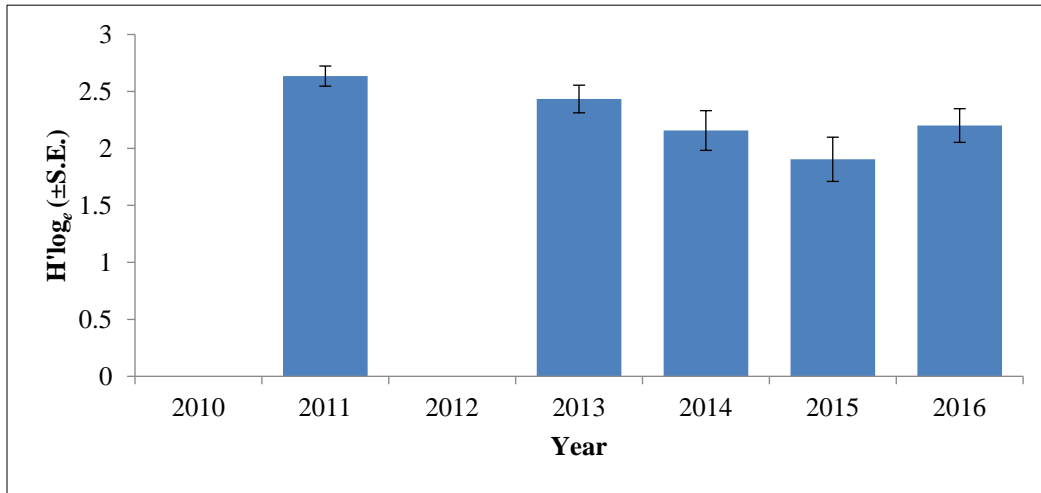


Figure 7. Shannon diversity ($H' \log_e$) of non-impacted sites post-spill.
Error bars represent one standard error.

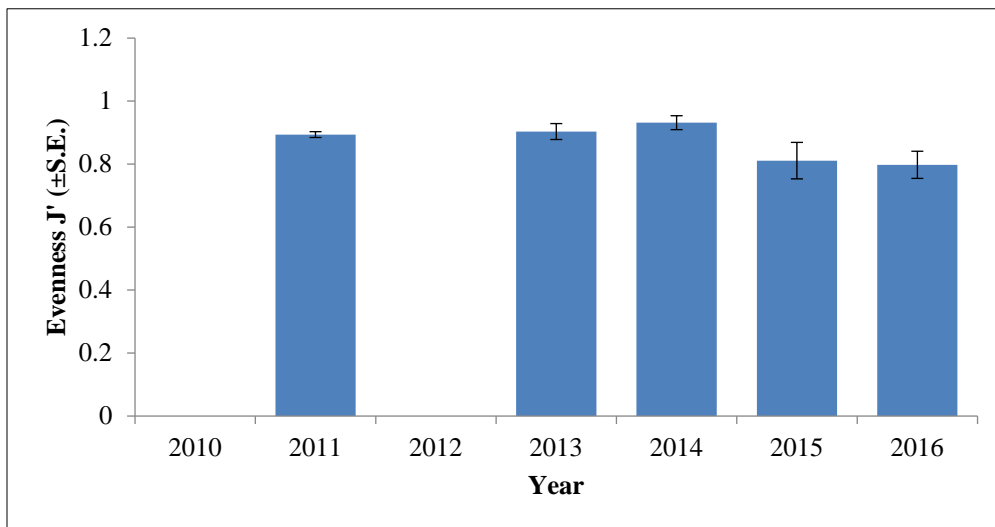


Figure 8. Taxa evenness (Pielou's J') of non-impacted sites post-spill.
Error bars represent one standard error.

Overall taxa composition varied between years at non-impacted sites (Figure 9). Polychaetes dominated communities in 2011–2014 (43–58%), while crustaceans dominated communities in 2015 and 2016 (42–53%). Multivariate community structure at non-impacted sites varied between years (Figure 10; Two-way ANOSIM, $R=0.24$, $p=0.0004$) and between sites (Two-way ANOSIM, $R=0.47$, $p=0.001$). However, the only significant pairwise comparisons were 2011 with 2014 and 2011 with 2016 ($R>0.38$, $p<0.01$) and were due to higher densities of oligochaetes, bivalves, Tanaellidae tanaids, and Syllidae polychaetes in 2011 than in 2014 (17.7% dissimilarity) but lower densities of Desmosomatidae isopods, Tanaid sp. B, and Dorvilleidae polychaetes than in 2016 (17.2% dissimilarity).

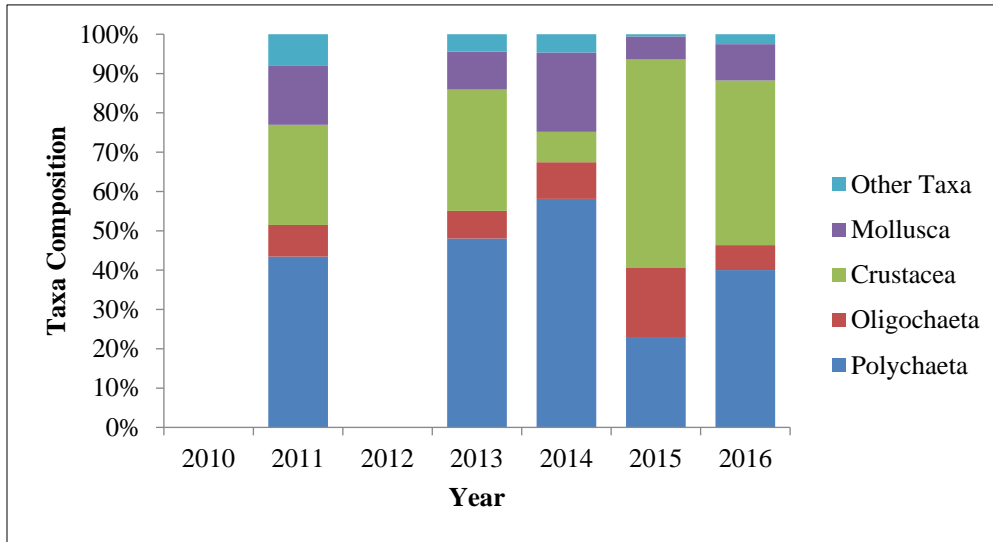


Figure 9. Percent taxonomic composition of macrofaunal abundance of non-impacted sites post-spill.

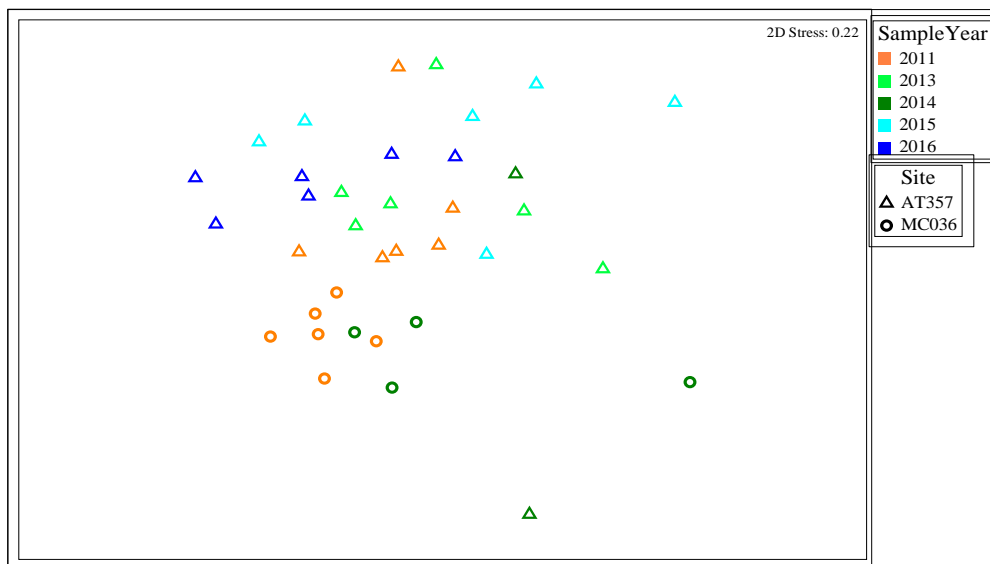


Figure 10. Non-metric multidimensional scaling of non-impacted communities post-spill. Based on Bray-Curtis similarities of square-root transformed abundance data.

3.3 Temporal Change in Impacted Communities

Macrofaunal density at the three impacted sites (MC297, MC294, and MC344) decreased over time since the spill (Figure 11; Pearson correlation = -0.31, $p=0.002$, $R^2=0.096$). Mean density was highest immediately after the spill in 2010 ($19,905 \pm 2,754$ individuals m^{-2}) and lowest in 2015 ($8,741 \pm 1,821$ individuals m^{-2}), with 2010 significantly higher than 2013, 2014, and 2015 (Tukey HSD, $p<0.029$) and 2012 significantly higher than 2015 (Tukey HSD, $p=0.042$).

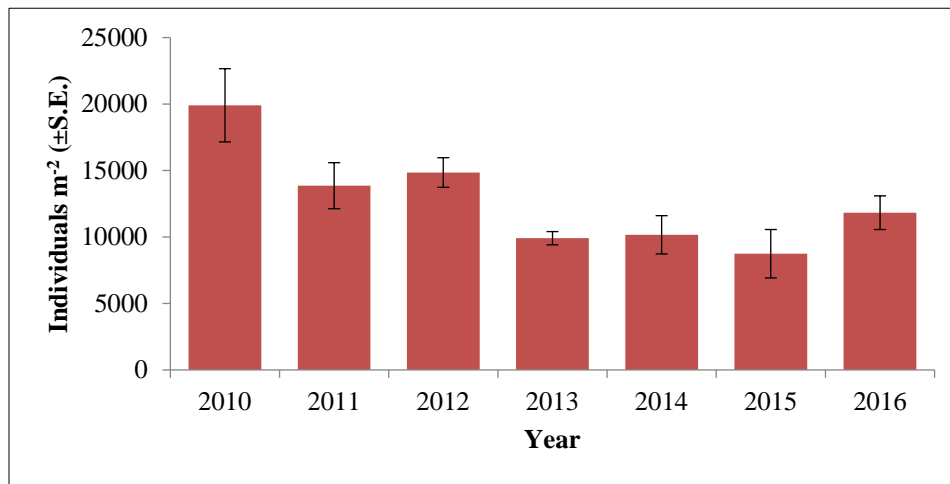


Figure 11. Macrofaunal density at impacted sites post-spill.
Error bars represent one standard error.

Diversity has remained stable over time. There was no significant correlation of Shannon diversity or taxa evenness with sample year (Spearman correlation: Shannon diversity $\rho=-0.113$, $p=0.27$; evenness $\rho=0.103$, $p=0.33$) and no significant difference among years (Figure 12; One-way ANOVA, $F_{6,87}=1.98$, $p=0.078$). However, taxa evenness did vary among years (Figure 13; One-way ANOVA, $F_{6,87}=3.43$, $p=0.004$), with 2010 significantly lower than all other years sampled (Tukey HSD, $p<0.042$).

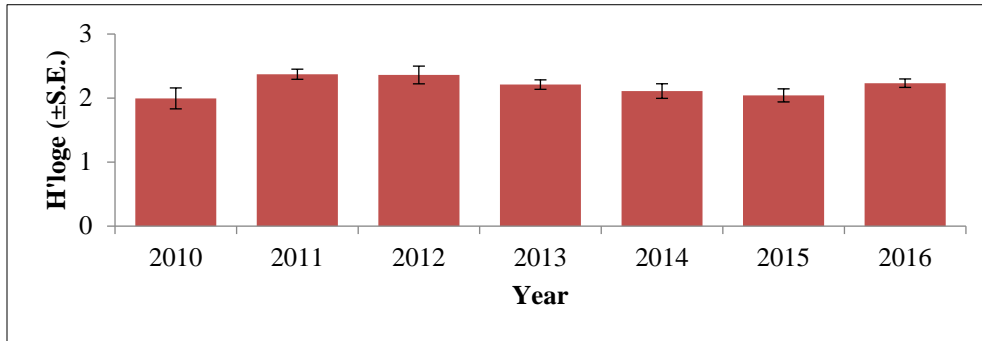


Figure 12. Shannon diversity ($H' \log_e$) at impacted sites post-spill.
Error bars represent one standard error.

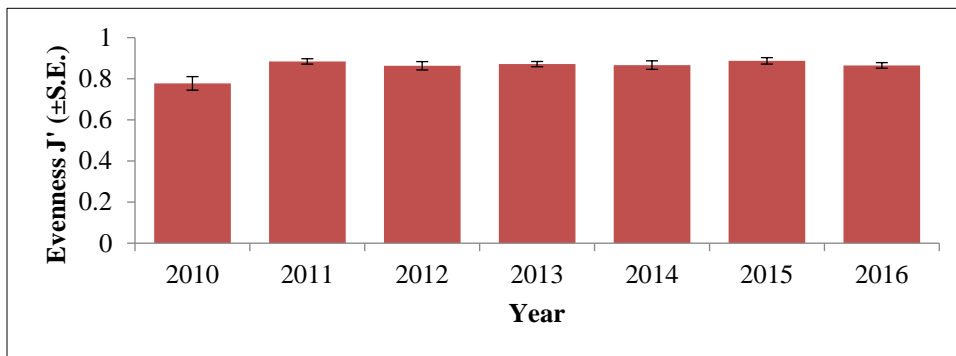


Figure 13. Taxa evenness (Pielou's J') at impacted sites post-spill.
Error bars represent one standard error.

Overall infaunal composition (Figure 14) varied among years, with 2010 being the most distinct with the highest proportions of polychaetes (84%), while the proportion of polychaetes for all other years ranged from 56 to 70%. In contrast, 2010 had the lowest proportion of crustaceans (4.6%) and molluscs (4.8%), while all other years ranged from 13 to 21% for crustacea and 14 to 21% for molluscs. Multivariate community structure also varied among years (Figure 15; Two-way ANOSIM, $R=0.208$, $p=0.00002$) as well as among sites (Two-way ANOSIM, $R=0.444$, $p=0.00001$), with communities in 2010 significantly different from all other years except 2012 ($R>0.19$, $p<0.048$). Macrofaunal communities from 2010 were dissimilar from other years due to higher densities of Dorvilleidae, Capitellidae, and Cirratulidae polychaetes and lower densities of Paraonidae polychaetes; those four taxa accounted for 25 to 31% of the dissimilarity between years. Pairwise comparisons also indicated that the only years that did not differ from one another were 2011 with 2012, 2014, and 2015 ($R>0.058$, $p>0.12$), and 2012 with 2014 ($R=0.14$, $p=0.13$). However, the first year post-spill (2010) and the most recently sampled year (2016) were still significantly different ($R=0.214$, $p=0.006$).

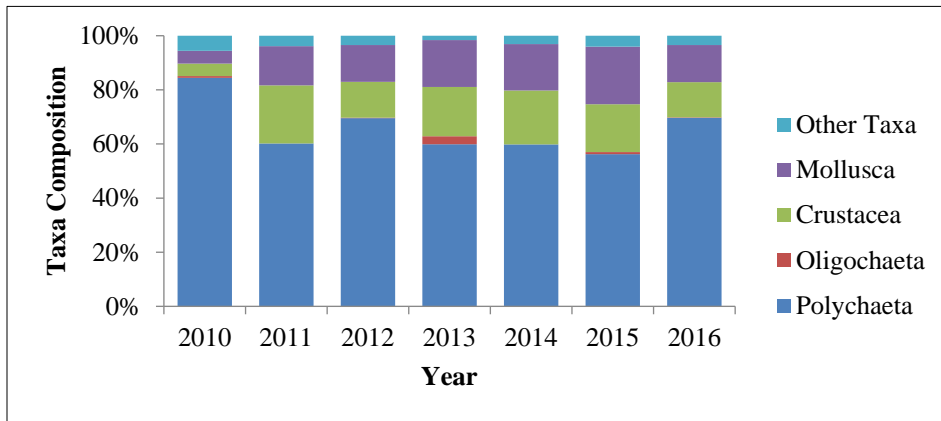


Figure 14. Percent taxonomic composition of macrofaunal abundance at impacted sites post-spill.

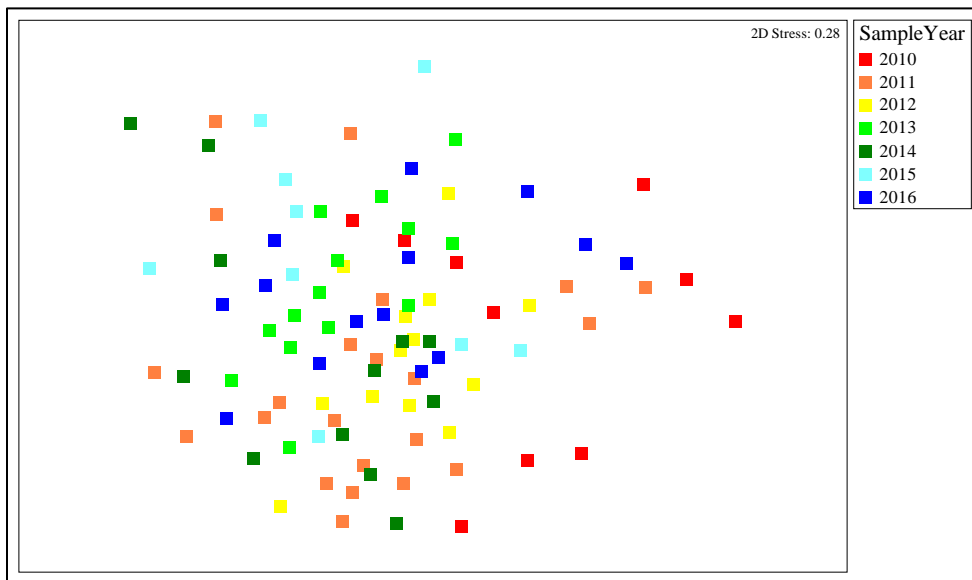


Figure 15. Non-metric multidimensional scaling of impacted communities post-spill.
Based on Bray-Curtis similarities of square-root transformed abundance data.

3.4 Impacted and Non-Impacted Communities

Macrofaunal density did not differ between impacted and non-impacted communities within years sampled (One-way ANOVA, $p > 0.05$). In contrast, Shannon diversity was significantly lower in 2011 at impacted sites than non-impacted sites (One-way ANOVA, $F_{1,32} = 4.38$, $p = 0.044$) but the remaining years were similar. Taxa evenness was also similar between impacted and non-impacted sites within years (One-way ANOVA, $p > 0.07$). Multivariate analysis of community assemblages yielded differences between impacted and non-impacted sediments even after accounting for variability among years (Figure 16; Two-way ANOSIM: Impact $R = 0.287$, $p = 0.00001$).

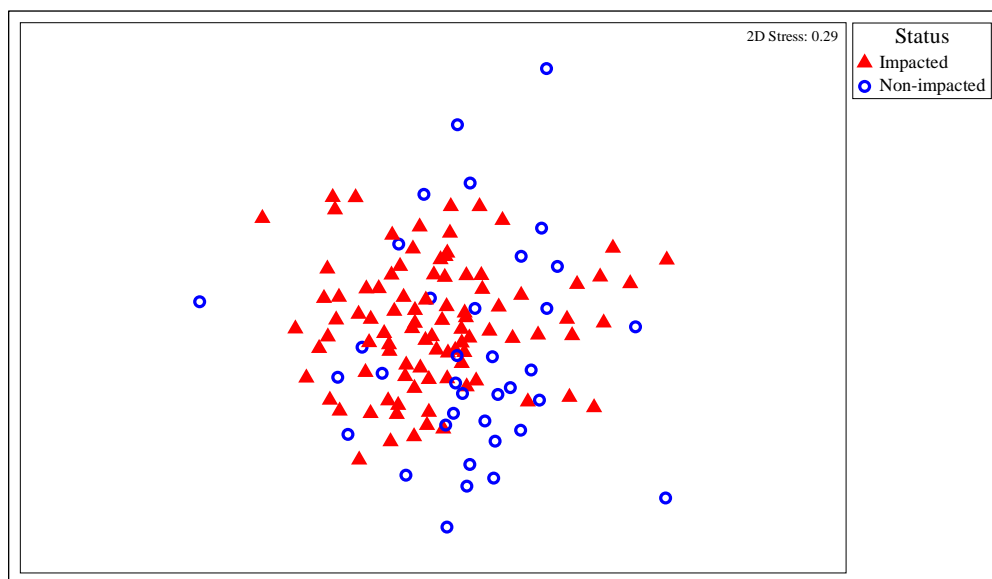


Figure 16. Non-metric multidimensional scaling of impacted and non-impacted communities post-spill.

Based on Bray-Curtis similarities of square-root transformed abundance data.

3.5 Environmental Variables

Various geochemical analyses were performed on surface sediment sections (0–1 or 0–2 cm, depending on the sample) from both the impacted and non-impacted sites. Sediment grain size at impacted sites contained high proportions of mud for all years sampled (Figure 17; $> 97\%$). In contrast, non-impacted sites had lower mud content (73–93%) and higher sand (6–18%) and gravel (1–20%) content. Organic carbon content was highest in 2011 at impacted sites (Figure 18; $1.50 \pm 0.1\%$) and significantly decreased over time (Spearman correlation, $\rho = -0.57$, $p = 0.008$). At non-impacted sites, organic carbon content was also highest in 2011 ($1.29 \pm 0.2\%$), but there was no correlation with time (Spearman correlation, $\rho = -0.43$, $p = 0.24$). Stable carbon isotope composition also decreased over time at impacted sites (Figure 19; Spearman correlation, $\rho = -0.45$, $p = 0.048$), but not at non-impacted sites (Spearman correlation, $\rho = -0.19$, $p = 0.62$). Overall, the $\delta^{13}\text{C}$ was higher at impacted sites than non-impacted sites.

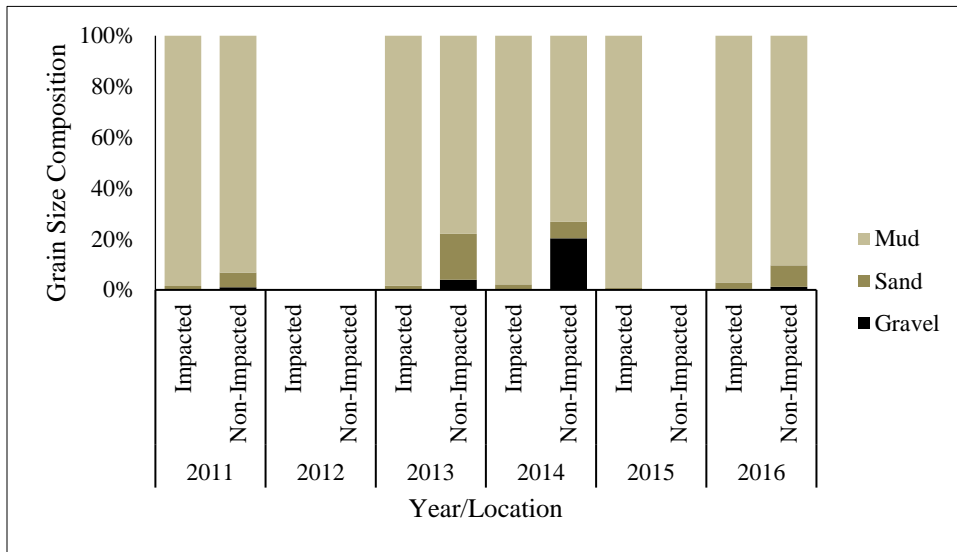


Figure 17. Sediment grain size composition of surface sediment at impacted and non-impacted sites post-spill.

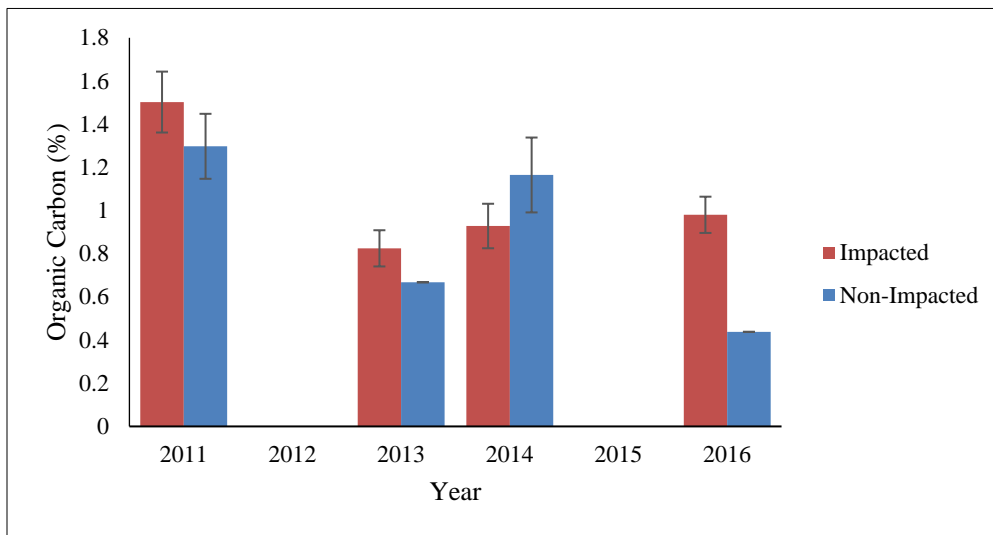


Figure 18. Sediment organic carbon content (%) of surface sediment at impacted and non-impacted sites post-spill.

Error bars represent one standard error.

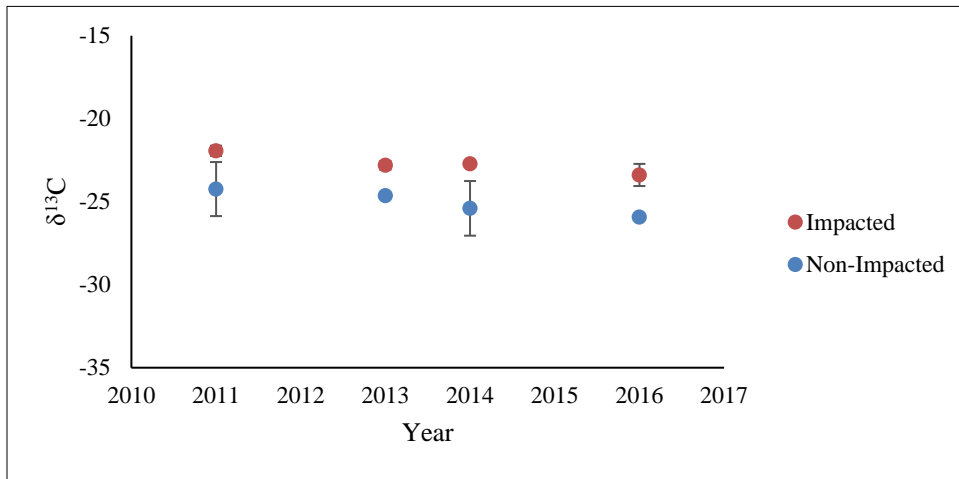


Figure 19. Sediment stable carbon isotopic composition ($\delta^{13}\text{C}$) of surface sediment at impacted and non-impacted sites post-spill.

Error bars represent one standard error.

DISTLM analysis indicated that all variables except organic carbon content and sample year could individually explain a significant portion of the variation in impacted and non-impacted communities (Table 2), with mud content providing the best individual explanation (11.4%, $p=0.014$). The “best” model included mud content, depth, and $\delta^{13}\text{C}$, explaining 28.4% of the variation in impacted and non-impacted communities (Table 3; Figure 20). However, 15 additional models were within 1 AICc unit of the “best” model, with the five-variable model of mud content, latitude, longitude, depth, and $\delta^{13}\text{C}$ explaining 40.2% of the community variation.

Table 2. DISTLM Results of Environmental Variables for Impacted and Non-impacted Sites Post-spill

SS(trace)= quantitative partition of the total sum of squares for each variable; Pseudo-F= F statistic; P= p-value of the Pseudo-F statistic; Proportion= proportion of the community variation explained by the individual variable.

Variable	SS (trace)	Pseudo-F	P	Proportion
Mud	4,760	3.475	0.0141	0.1140
Year	1,634	1.100	0.3453	0.0391
Latitude	4,054	2.904	0.0001	0.0971
Longitude	4,219	3.036	0.0001	0.1011
Depth	3,887	2.772	0.0001	0.0931
$\delta^{13}\text{C}$	3,678	2.609	0.0005	0.0881
%C	1,788	1.208	0.2329	0.0428
Total	41,741			

Table 3. DISTLM Results of “Best” Models of Environmental Variables for Impacted and Non-impacted Post-spill Sites

R²= proportion of community variation explained by the model; RSS=residual sum of squares; No.Vars= number of variables in the model.

AICc	R ²	RSS	No.Vars	Selections
210.86	0.2842	29,879	3	Mud, Depth, δ ¹³ C
211.03	0.2800	30,054	3	Mud, Latitude, Depth
211.04	0.2093	33,006	2	Mud, Longitude
211.07	0.2084	33,041	2	Mud, δ ¹³ C
211.08	0.2082	33,052	2	Mud, Latitude
211.09	0.2784	30,122	3	Mud, Latitude, Longitude
211.15	0.2771	30,177	3	Mud, Longitude, Depth
211.26	0.3443	27,370	4	Mud, Latitude, Longitude, δ ¹³ C
211.39	0.3412	27,500	4	Mud, Latitude, Depth, δ ¹³ C
211.41	0.2704	30,456	3	Mud, Longitude, δ ¹³ C
211.45	0.1980	33,475	2	Mud, Depth
211.55	0.2669	30,600	3	Mud, Latitude, δ ¹³ C
211.60	0.3364	27,699	4	Mud, Longitude, Depth, δ ¹³ C
211.79	0.3322	27,876	4	Mud, Latitude, Longitude, Depth
211.80	0.4020	24,963	5	Mud, Latitude, Longitude, Depth, δ ¹³ C
211.84	0.1140	36,981	1	Mud

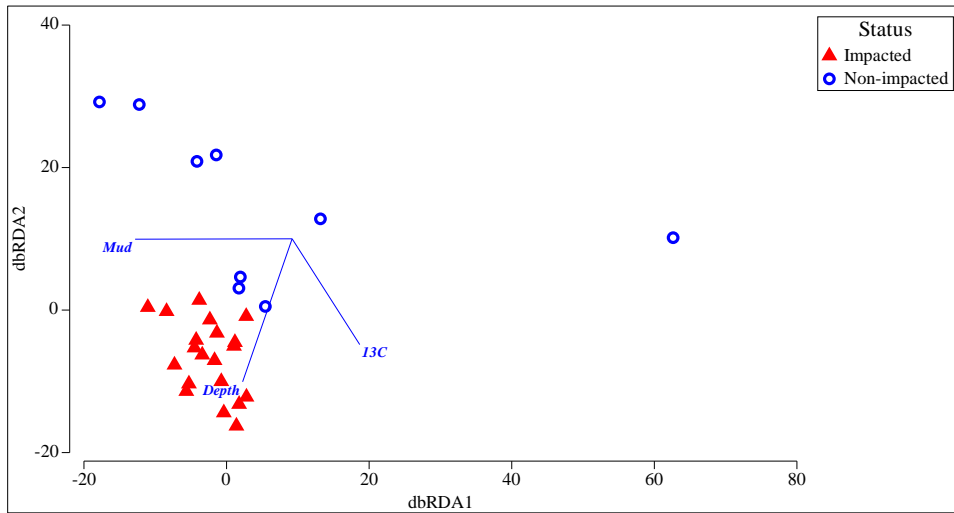


Figure 20. dbRDA of the “best” model of environmental variables explaining impacted and non-impacted communities post-spill.

Based on Bray-Curtis similarities of square-root transformed abundance data. Axis dbRDA1 accounts for 42.4% of the fitted and 12% of the total variation, and axis dbRDA2 accounts for 36.1% of the fitted and 10.3% of the total variation.

3.6 Comparisons to Other Gulf of Mexico Habitats

Coral-associated sediment communities, whether they were from impacted or non-impacted sites, were distinct from other habitat types in the Gulf, including chemosynthetic seeps, shipwrecks, and soft-sediments (Figure 21; One-way ANOSIM, $R > 0.365$, $p < 0.0004$). Impacted communities were most similar to the nearby non-impacted communities ($R = 0.187$, $p = 0.0003$) and reference coral communities ($R = 0.306$, $p = 0.00001$), but differed significantly from soft-sediment communities ($R = 0.799$, $p = 0.00001$).

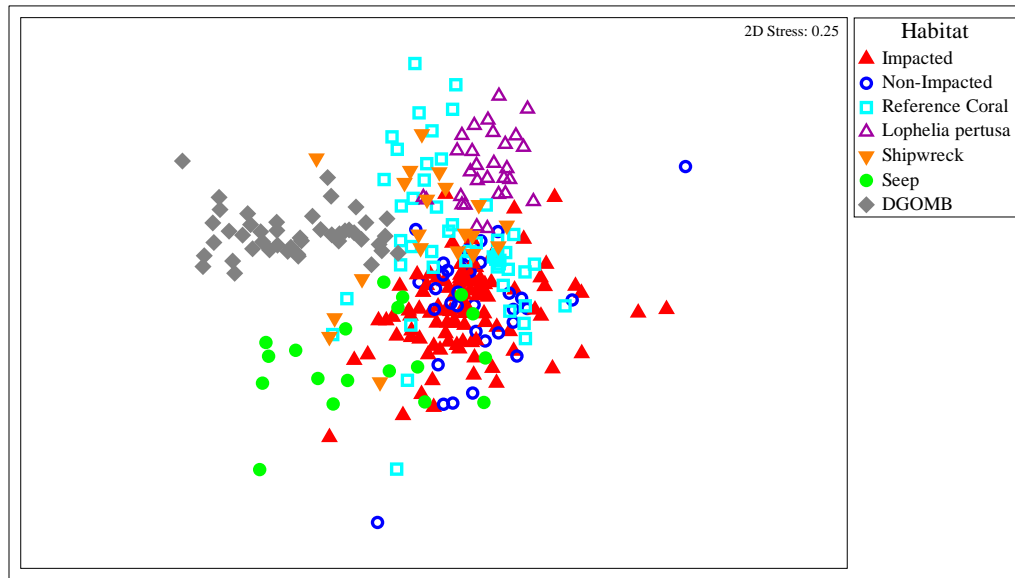


Figure 21. Non-metric multidimensional scaling of multiple deep-sea habitats in the Gulf of Mexico.

Based on Bray-Curtis similarities of square-root transformed abundance data. Impacted sites include MC294, MC297, and MC344. Non-impacted sites include MC036 and AT357. Reference corals and *Lophelia pertusa* cores from Bourque and Demopoulos (2018); Shipwreck cores from Demopoulos et al. (2017); Seep cores from Brooks et al. (2014); DGOMB cores from Rowe and Kennicutt II (2009).

4 Discussion

4.1 Pre-spill and Post-spill Reference Communities

Although little information was available on pre-spill coral infaunal communities, temporal dynamics pre- and post-spill in healthy coral communities differed for octocorals and *L. pertusa* habitats. There was no change in either the univariate metrics (e.g., density, diversity) or community structure between the pre-spill and post-spill samples at the reference octocoral site, but there was a difference in evenness and community structure at the *L. pertusa* sites. Despite the significant difference in *L. pertusa* communities between time points, the small R value (see 3.1.2) suggests the overall difference was small, and all *L. pertusa* communities clustered together when compared to all other Gulf habitats (Figure 21). There are several potential reasons for the different temporal dynamics at these two habitats. First, infaunal communities at *L. pertusa* and octocoral habitats are known to differ in the Gulf, with higher sediment organic content and coarse-grained sediments (Bourque and Demopoulos 2018), thus year-to-year change might also be dissimilar, as observed. Second, the time span between sampling points at *L. pertusa* habitats (2 years) was greater than for the octocoral habitat (1 year), which might account for the higher dissimilarity at *L. pertusa* communities. Additional time-series sampling at undisturbed reference coral locations of multiple coral types would help define long-term (>2 years) natural temporal change in Gulf coral communities.

The observed stability in communities at the octocoral site suggests that in areas not impacted by the *Deepwater Horizon* spill, there was little temporal change in coral-associated sediment communities in the year just before and just after the spill. In the absence of disturbance events, temporal variability of macrofauna in the deep sea is expected to be low, with change often structured by seasonal fluctuations of surface productivity export to the sea floor (e.g., Tyler 1988). However, the location of the octocoral site, GB299, may provide limited insights into temporal dynamics at the deeper impacted sites. Both coral and soft-sediment communities vary in the Gulf based on depth and location (Wei et al. 2010, Bourque and Demopoulos 2018), and GB299 is 397 kilometers from the spill site at MC252 and at least 384 kilometers from the impacted sites. Additionally, GB299 occurs at a depth of 355 m, far shallower than the 1,300 m of the shallowest impacted site. The impacted sites are also at deeper depths (>1,300 m) than previously investigated coral infaunal communities (<1,100 m; Bourque and Demopoulos 2018) and the natural patterns in community structure (e.g., density, diversity) at these depths has yet to be established. However, the deep sea is a relatively stable environment, such that we might expect community variability would decrease at increased depths. Therefore, communities examined at GB299 provide a conservative baseline estimate for variability at the deep impacted sites. The lack of pre-spill information of communities near the wellhead highlights the importance of this pre- and post-spill baseline information to provide context for detailed post-spill analysis of communities of impacted and non-impacted sites.

4.2 Temporal Change at Impacted Sites and Non-impacted Sites

Patterns in community parameters (e.g., density, diversity, community structure) differed between impacted and non-impacted sites, suggesting different environmental controls on these communities. Density was highest at the impacted sites immediately after the spill; however, this was only at a single impacted site. The initial high density and low diversity suggests an organic enrichment response, with communities dominated by tolerant taxa (Fisher et al. 2014). The decline in density from 2010 to 2011

suggests an overall toxicity response that was not immediate, likely related to continued deposition of hydrocarbons from the deep-water plume over time, with densities remaining low through 2015. In contrast, macrofaunal density did not change over time at the non-impacted sites, suggesting an overall stability in natural communities in the years following the spill, consistent with our results from the healthy coral habitat at GB299. Diversity patterns also differed between impacted and non-impacted communities, with diversity decreasing over time at non-impacted sites, but no overall change at impacted sites. Community structure differed among years for both impacted and non-impacted sites, but again, the pattern of change differed. At the impacted sites, most years differed from each other, another indication of a constantly changing community. In contrast, community differences at the non-impacted sites were determined by a difference between 2011 with 2014 and 2016, suggesting that there are longer-term natural changes occurring in reference coral habitats that persist over time.

Multiple factors influenced the community dynamics at impacted and non-impacted sites post-spill. Consistent with previous studies (e.g., Demopoulos et al. 2014, Demopoulos et al. 2016, Bourque and Demopoulos 2018), sampling location, which also corresponded to depth differences, is a significant factor in structuring communities accounting for a larger difference than between years. The DISTLM analysis indicated that depth, percent mud content, and stable carbon isotope composition are the specific site parameters structuring communities. Depth has previously been identified as a structuring agent on Gulf coral communities (Bourque and Demopoulos 2018), and the effect of depth may confound our results, as depth is unique for the impacted sites, with all non-impacted sites occurring at shallower depths. Additional samples from non-impacted coral sites at similar depths as the impacted sites would allow for an estimation of the overall effect of depth on coral sediment communities. Mud content was also higher at impacted sites than non-impacted sites, possibly due to increased sedimentation of fine-grained material from the *Deepwater Horizon* blowout in proximity to the wellhead. The higher proportion of sand and gravel-sized sediments at non-impacted sites are likely the result of the multiple coral types present at AT357, including the scleractinian *M. oculata*, which is prone to breakage providing a source of large grain sizes to adjacent sediments. Lastly, the $\delta^{13}\text{C}$ values were lower at non-impacted sites as compared to impacted sites, suggesting different carbon sources. Many of the coral sites also contain natural hydrocarbon seeps (e.g., MC344, AT357), with high concentrations of hydrocarbons in subsurface sediment (5-10 cm; Fisher et al. 2014) as compared to surface sediments which might account for the different isotopic composition. Variable deposition of fresh material from surface productivity to the seafloor may also account for the different sediment $\delta^{13}\text{C}$ values between impacted and non-impacted sites, where fresh organic matter is enriched in ^{13}C relative to sediments associated with hydrocarbon seeps (Demopoulos et al. 2010). Overall, differences in the local sediment environment between impacted and non-impacted sites continued to persist over time, influencing the associated infaunal communities.

Because only a few other studies have documented temporal changes in *Deepwater Horizon*-affected benthic communities post-spill (Fisher et al. 2014, Montagna et al. 2016, Qu et al. 2016), comparisons are limited for coral-associated sediment communities. High hydrocarbon concentrations documented at the impacted sites in 2011 by Fisher et al. (2014) are consistent with the results of Montagna et al. (2016), indicating a regional deposition of hydrocarbons near the wellhead. However, macrofaunal community metrics at impacted coral sites differed from impacted soft-sediments, which had increases in both density and diversity between 2010 and 2011 (Montagna et al. 2016). Although sampling effort in 2010 for coral communities was limited, the difference in community response between soft-sediments and coral communities suggest different recovery trajectories for these environments, which can only be determined by additional sampling of soft-sediments post-spill. Given the different depositional environment surrounding deep-sea corals (e.g., Mienis et al. 2009, Mienis et al. 2009, Mienis et al. 2012), the initial supply and concentration of hydrocarbons following the spill may have differed for coral habitats and was

likely patchy in nature (Valentine et al. 2014), resulting in high concentrations at farther distances from the wellhead than for soft-sediment habitats (Montagna et al. 2013, Fisher et al. 2014). Once deposited, hydrocarbons are broken down by microbial processes and slowly buried by natural sediment deposition. Natural sediment deposition rates in the Gulf are low (Yeager et al. 2004), suggesting burial of hydrocarbons will be slow. The continued high levels of hydrocarbons at MC294 (Fisher et al., 2014) is consistent with the results of Montagna et al. (2016), who suggest that hydrocarbon concentrations would continue to remain above background levels for many years. Continued high levels of hydrocarbons, combined with potentially low burial rates, would enable long-term exposure of infaunal taxa to hydrocarbons, possibly resulting in the continual decline in macrofaunal density at the impacted coral sites.

4.3 Other Habitats in the Gulf of Mexico

Because the pre-spill community baseline was unknown at any of the impacted sites, it is unclear what a recovered community at these sites should resemble. However, our results indicate that impacted communities continued to change seven years post-spill, while communities at non-impacted sites exhibited few changes. Compared to other types of benthic habitats in the Gulf (e.g., chemosynthetic seeps, *L. pertusa*, shipwrecks, soft-sediments), impacted communities most closely resemble reference and non-impacted coral communities. Coral communities continue to differ from historical Gulf soft-sediment environments irrespective of their location (Rowe and Kennicutt II 2009), consistent with previous work (Demopoulos et al. 2014, Fisher et al. 2014), highlighting the importance of these unique communities to the biodiversity of the Gulf region as a whole. Thus, monitoring changes in non-impacted habitats provides the baseline data and metrics needed for documenting response and quantifying recovery at impacted sites.

Loss of benthos following a disturbance event like the *Deepwater Horizon* spill has broader ecological impacts because benthic fauna provide important ecosystem services, including organic matter decomposition, bioturbation and stabilization of sediments, and transfer of energy to higher trophic levels (Danovaro et al. 2008). As coral sediments differ from the vast soft sediments of the Gulf with individual sites isolated from one another, the magnitude of impact is likely greater than for soft-sediments as recovery will be determined in part by recruitment and succession. With multiple unique taxa occurring in deep-sea coral sediments, loss of biodiversity may be greater because macrofauna often have limited dispersal ranges. In addition, because the corals themselves have been injured at many of these sites, we have yet to determine how a change in the local physical habitat heterogeneity may contribute to recovery trajectories.

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Appendix A: Sample Location Information

Table A-1. Parameters associated with each sediment core included in analyses

RB=NOAA Ship *Ronald H. Brown*; SJ=R/V *Seward Johnson*; HC=*Holiday Chouest*; NA=E/V *Nautilus*; AT=R/V *Atlantis*; FK=R/V *Falkor*; Gyre=R/V *Gyre*; CH=R/V *Cape Hatteras*; Jason=ROV *Jason II*; BC=Box core; JSL=HOV *Johnson Sea Link II*; Mill=ROV *Millennium*; Herc=ROV *Hercules*; Alvin=HOV *Alvin*; OI=DSV *Ocean Inspector*; GEX=ROV *Global Explorer*; Infauna=number of cores used for infaunal analyses; GC=number of cores used in environmental analyses.

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
Impacted temporal site	MC294	2010	AT/Alvin	28.6721	-88.4764	1,369	3		Fisher et al. 2014
Impacted temporal site	MC294	2010	AT/Alvin	28.6722	-88.4765	1,370	3		Fisher et al. 2014
Impacted temporal site	MC294	2010	AT/Alvin	28.6723	-88.4764	1,373	4		Fisher et al. 2014
Impacted temporal site	MC294	2011	HC/Mill	28.6721	-88.4764	1,372	3	1	Fisher et al. 2014, Demopoulos et al. 2016
Impacted temporal site	MC294	2011	HC/Mill	28.6722	-88.4764	1,372	3	1	Fisher et al. 2014, Demopoulos et al. 2016
Impacted temporal site	MC294	2012	FK/GEX	28.6721	-88.4764	1,371	3		This study
Impacted temporal site	MC294	2013	NA/Herc	28.6724	-88.4770	1,370	4	1	This study
Impacted temporal site	MC294	2014	NA/Herc	28.5891	-88.4765	1,370	4	1	This study
Impacted temporal site	MC294	2015	NA/Herc	28.6726	-88.4765	1,370	4		This study
Impacted temporal site	MC294	2016	OI/GEX	28.6722	-88.4766	1,381	2	1	This study
Impacted temporal site	MC294	2016	OI/GEX	28.6721	-88.4765	1,381	3	1	This study
Impacted temporal site	MC297	2011	HC/Mill	28.6961	-88.3463	1,550	4	1	Demopoulos et al. 2016
Impacted temporal site	MC297	2011	HC/Mill	28.6822	-88.3450	1,586	3	1	Demopoulos et al. 2016
Impacted temporal site	MC297	2011	HC/Mill	28.6814	-88.3440	1,578	3	1	Demopoulos et al. 2016
Impacted temporal site	MC297	2012	FK/GEX	28.6824	-88.4493	1,548	3		This study
Impacted temporal site	MC297	2012	FK/GEX	28.6824	-88.3449	1,584	4		This study
Impacted temporal site	MC297	2013	NA/Herc	28.6822	-88.3449	1,584	4	1	This study
Impacted temporal site	MC297	2013	NA/Herc	28.6798	-88.3422	1,570	2	1	This study

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
Impacted temporal site	MC297	2014	NA/Herc	28.6820	-88.3450	1,583	4	1	This study
Impacted temporal site	MC297	2015	NA/Herc	28.6822	-88.3452	1,584	3		This study
Impacted temporal site	MC297	2016	OI/GEX	28.6799	-88.3422	1,573	2	1	This study
Impacted temporal site	MC297	2016	OI/GEX	28.6822	-88.3450	1,587	3	1	This study
Impacted temporal site	MC344	2011	HC/Mill	28.6338	-88.1697	1,857	3	1	Demopoulos et al. 2016
Impacted temporal site	MC344	2011	HC/Mill	28.6336	-88.1695	1,857	3	1	Demopoulos et al. 2016
Impacted temporal site	MC344	2012	FK/GEX	28.6335	-88.1694	1,853	3		This study
Impacted temporal site	MC344	2013	NA/Herc	28.6335	-88.1695	1,853	4	1	This study
Impacted temporal site	MC344	2014	NA/Herc	28.6338	-88.1698	1,853	4	1	This study
Impacted temporal site	MC344	2015	NA/Herc	28.6336	-88.1693	1,853	2		This study
Impacted temporal site	MC344	2016	OI/GEX	28.6338	-88.1699	1,852	2	1	This study
Impacted temporal site	MC344	2016	OI/GEX	28.6335	-88.1695	1,857	2	1	This study
Non-impacted temporal site	MC036	2011	HC/Mill	28.9354	-88.2014	1,094	3	1	Demopoulos et al. 2016
Non-impacted temporal site	MC036	2011	HC/Mill	28.9354	-88.2027	1,094	3	1	Demopoulos et al. 2016
Non-impacted temporal site	MC036	2014	NA/Herc	28.9354	-88.2027	1,094	4	1	Bourque and Demopoulos 2018
Non-impacted temporal site	AT357	2011	HC/Mill	27.5865	-89.7045	1,051	3	1	Bourque and Demopoulos 2018
Non-impacted temporal site	AT357	2011	HC/Mill	27.5866	-89.7041	1,048	3	1	Fisher et al. 2014, Demopoulos et al. 2016
Non-impacted temporal site	AT357	2013	NA/Herc	27.5867	-89.7046	1,049	3	1	Bourque and Demopoulos 2018
Non-impacted temporal site	AT357	2013	NA/Herc	27.5857	-89.7050	1,054	3	1	Bourque and Demopoulos 2018
Non-impacted temporal site	AT357	2014	AT/Alvin	27.5864	-89.7044	1,050	1	1	Bourque and Demopoulos 2018
Non-impacted temporal site	AT357	2014	AT/Alvin	27.5861	-89.7044	1,054	1	1	Bourque and Demopoulos 2018
Non-impacted temporal site	AT357	2015	NA/Herc	27.5868	-89.7045	1,049	1		This study

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
Non-impacted temporal site	AT357	2015	NA/Herc	27.5859	-89.7048	1,055	1		This study
Non-impacted temporal site	AT357	2015	NA/Herc	27.5857	-89.7051	1,056	1		This study
Non-impacted temporal site	AT357	2015	NA/Herc	27.5862	-89.7048	1,052	1		This study
Non-impacted temporal site	AT357	2015	NA/Herc	27.5865	-89.7039	1,048	1		This study
Non-impacted temporal site	AT357	2015	NA/Herc	27.5868	-89.7047	1,050	1		This study
Non-impacted temporal site	AT357	2016	OI/GEX	27.5858	-89.7050	1,064	1		This study
Non-impacted temporal site	AT357	2016	OI/GEX	27.5867	-89.7047	1,057	2	1	This study
Non-impacted temporal site	AT357	2016	OI/GEX	27.5866	-89.7046	1,056	1		This study
Non-impacted temporal site	AT357	2016	OI/GEX	27.5868	-89.7047	1,048	2		This study
Reference coral site	AT47	2009	RB/Jason	27.8802	-89.7888	840	3		Bourque and Demopoulos 2018
Reference coral site	GB299	2009	RB/Jason	27.6863	-92.2308	359	5		Bourque and Demopoulos 2018
Reference coral site	GB299	2010	RB/Jason	27.6866	-92.2310	362	3		Bourque and Demopoulos 2018
Reference coral site	GB299	2010	RB/Jason	27.6865	-92.2307	361	3		Bourque and Demopoulos 2018
Reference coral site	GB299	2010	RB/Jason	27.6846	-92.2209	340	2		Bourque and Demopoulos 2018
Reference coral site	GC140	2010	RB/Jason	27.8108	-91.5371	263	2		Bourque and Demopoulos 2018
Reference coral site	GC249	2010	RB/Jason	27.7241	-90.5142	789	3		Bourque and Demopoulos 2018
Reference coral site	MC118	2010	RB/Jason	28.8527	-88.4925	883	3		Bourque and Demopoulos 2018
Reference coral site	MC118	2010	RB/Jason	28.8527	-88.4927	882	3		Bourque and Demopoulos 2018
Reference coral site	MC118	2011	HC/Mill	28.8526	-88.4926	887	3		Bourque and Demopoulos 2018
Reference coral site	MC118	2011	HC/Mill	28.8560	-88.4936	888	3		Demopoulos et al. 2016
Reference coral site	MC118	2013	NA/Herc	28.8528	-88.4927	884	3		Bourque and Demopoulos 2018
Reference coral site	MC118	2013	NA/Herc	28.8527	-88.4925	883	1		Bourque and Demopoulos 2018
Reference coral site	MC203	2011	HC/Mill	28.7873	-88.6347	919	3		Demopoulos et al. 2016

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
Reference coral site	MC507	2011	HC/Mill	28.4855	-88.8508	1,043	3		Fisher et al. 2014, Demopoulos et al. 2016
Reference coral site	MC885	2010	RB/Jason	28.0664	-89.7170	633	3		Bourque and Demopoulos 2018
Reference coral site	MC885	2014	AT/Alvin	28.0661	-89.7172	634	1		Bourque and Demopoulos 2018
Reference coral site	MC885	2014	AT/Alvin	28.0661	-89.7173	635	1		Bourque and Demopoulos 2018
<i>Lophelia pertusa</i> site	MC751	2009	RB/Jason	28.1937	-89.7988	440	3		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK826	2009	RB/Jason	29.1578	-88.0162	475	3		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK826	2009	RB/Jason	29.1582	-88.0168	470	2		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK826	2009	RB/Jason	29.1587	-88.0104	480	2		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK826	2011	HC/Mill	29.1650	-88.0115	464	4		Bourque and Demopoulos 2018
<i>Lophelia pertusa</i> site	VK906	2009	RB/Jason	29.0696	-88.3771	388	3		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK906	2009	RB/Jason	29.0692	-88.3776	393	3		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK906	2009	RB/Jason	29.0690	-88.3771	392	3		Demopoulos et al., 2014
<i>Lophelia pertusa</i> site	VK906	2011	HC	29.0699	-88.3776	402	3		Bourque and Demopoulos 2018
<i>Lophelia pertusa</i> site	VK906	2011	HC	29.0694	-88.3775	392	3		Bourque and Demopoulos 2018
Seep site	AC601	2007	CH/BC	26.3901	-94.5133	2,384	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6462	-88.3635	2,239	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6465	-88.3664	2,222	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6466	-88.3752	2,207	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6451	-88.3614	2,222	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6447	-88.3677	2,222	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6458	-88.3661	2,227	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6441	-88.3638	2,255	1		Brooks et al. 2014
Seep site	AT340	2007	CH/BC	27.6475	-88.3747	2,222	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1166	-91.1640	1,431	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1192	-91.1660	1,426	1		Brooks et al. 2014

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
Seep site	GC852	2007	CH/BC	27.1163	-91.1646	1,435	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1210	-91.1666	1,449	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1200	-91.1651	1,425	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1113	-91.1653	1,431	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1109	-91.1666	1,406	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1091	-91.1659	1,400	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1185	-91.1665	1,430	1		Brooks et al. 2014
Seep site	GC852	2007	CH/BC	27.1201	-91.1651	1,425	1		Brooks et al. 2014
Shipwreck site	Ewing	2009	RB/Jason	28.0	-90.1	622	4		Demopoulos et al. 2017
Shipwreck site	Green Lantern	2009	RB/Jason	27.7	-90.7	913	4		Demopoulos et al. 2017
Shipwreck site	Gulfpenn	2009	RB/Jason	28.4	-89.3	557	4		Demopoulos et al. 2017
Shipwreck site	MC657	2009	RB/Jason	28.3	-87.9	2,270	4		Demopoulos et al. 2017
Shipwreck site	VK786	2009	RB/Jason	29.2	-87.8	613	5		Demopoulos et al. 2017
Shipwreck site	Gulf Oil	2010	RB/Jason	28.2	-89.8	532	4		Demopoulos et al. 2017
Shipwreck site	Monterrey	2013	NA/Herc	26.9	-93.1	1,330	2		Demopoulos et al. 2017
DGOMB	AC1	2000	Gyre/BC	26.3917	-94.5596	2,505	1		Rowe and Kennicutt II 2009
DGOMB	B1	2000	Gyre/BC	27.2031	-91.4040	2,260	1		Rowe and Kennicutt II 2009
DGOMB	B2	2000	Gyre/BC	26.5513	-92.2167	2,630	1		Rowe and Kennicutt II 2009
DGOMB	B3	2000	Gyre/BC	26.1644	-91.7351	2,650	1		Rowe and Kennicutt II 2009
DGOMB	C12	2000	Gyre/BC	26.3794	-89.2414	2,922	1		Rowe and Kennicutt II 2009
DGOMB	C12	2000	Gyre/BC	26.3829	-89.2414	2,920	1		Rowe and Kennicutt II 2009
DGOMB	C14	2000	Gyre/BC	26.9300	-89.5704	2,487	1		Rowe and Kennicutt II 2009
DGOMB	C14	2000	Gyre/BC	26.9298	-89.5645	2,487	1		Rowe and Kennicutt II 2009
DGOMB	C14	2000	Gyre/BC	26.9299	-89.5709	2,495	1		Rowe and Kennicutt II 2009
DGOMB	C4	2000	Gyre/BC	27.4532	-89.7631	1,455	1		Rowe and Kennicutt II 2009

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
DGOMB	C7	2000	Gyre/BC	27.7283	-89.9796	1,080	1		Rowe and Kennicutt II 2009
DGOMB	C7	2000	Gyre/BC	27.7329	-89.9772	1,070	1		Rowe and Kennicutt II 2009
DGOMB	GKF	2001	Gyre/BC	26.9272	-90.2106	2,452	1		Rowe and Kennicutt II 2009
DGOMB	HiPro	2001	Gyre/BC	28.5516	-88.5790	1,574	1		Rowe and Kennicutt II 2009
DGOMB	MT1	2000	Gyre/BC	28.5411	-89.8271	482	1		Rowe and Kennicutt II 2009
DGOMB	MT1	2000	Gyre/BC	28.5411	-89.8250	481	1		Rowe and Kennicutt II 2009
DGOMB	MT3	2000	Gyre/BC	28.2204	-89.4961	983	1		Rowe and Kennicutt II 2009
DGOMB	MT3	2000	Gyre/BC	28.2192	-89.4964	987	1		Rowe and Kennicutt II 2009
DGOMB	MT4	2000	Gyre/BC	27.8270	-89.1659	1,401	1		Rowe and Kennicutt II 2009
DGOMB	MT5	2000	Gyre/BC	27.3322	-88.6678	2,290	1		Rowe and Kennicutt II 2009
DGOMB	MT6	2000	Gyre/BC	27.0001	-87.9978	2,745	1		Rowe and Kennicutt II 2009
DGOMB	MT6	2000	Gyre/BC	27.0015	-87.9882	2,750	1		Rowe and Kennicutt II 2009
DGOMB	NB4	2000	Gyre/BC	26.2545	-92.3950	2,030	1		Rowe and Kennicutt II 2009
DGOMB	NB5	2000	Gyre/BC	26.2519	-91.2102	2,070	1		Rowe and Kennicutt II 2009
DGOMB	RW1	2000	Gyre/BC	27.5004	-96.0024	213	1		Rowe and Kennicutt II 2009
DGOMB	RW2	2000	Gyre/BC	27.2541	-95.7436	950	1		Rowe and Kennicutt II 2009
DGOMB	RW3	2000	Gyre/BC	27.0050	-95.5032	1,320	1		Rowe and Kennicutt II 2009
DGOMB	RW6	2000	Gyre/BC	26.0024	-94.4897	3,015	1		Rowe and Kennicutt II 2009
DGOMB	S1	2002	Gyre/BC	25.0070	-91.9994	3,528	1		Rowe and Kennicutt II 2009
DGOMB	S35	2000	Gyre/BC	29.3342	-87.0563	658	1		Rowe and Kennicutt II 2009
DGOMB	S36	2000	Gyre/BC	28.9194	-87.6704	1,825	1		Rowe and Kennicutt II 2009
DGOMB	S38	2000	Gyre/BC	28.2719	-87.3253	2,635	1		Rowe and Kennicutt II 2009
DGOMB	S39	2000	Gyre/BC	27.4992	-87.0014	3,007	1		Rowe and Kennicutt II 2009
DGOMB	S4	2002	Gyre/BC	24.2554	-85.4922	3,410	1		Rowe and Kennicutt II 2009
DGOMB	S40	2000	Gyre/BC	27.8389	-86.7526	2,975	1		Rowe and Kennicutt II 2009
DGOMB	S41	2000	Gyre/BC	28.0122	-86.5699	2,974	1		Rowe and Kennicutt II 2009

Habitat	Site	Year	Vessel/ Vehicle	Latitude (°N)	Longitude (°W)	Depth (m)	Infauna	GC	Source
DGOMB	S41	2001	Gyre/BC	27.9843	-86.5692	2,982	1		Rowe and Kennicutt II 2009
DGOMB	S42	2000	Gyre/BC	28.2526	-86.4178	767	1		Rowe and Kennicutt II 2009
DGOMB	S44	2000	Gyre/BC	28.7502	-85.7494	215	1		Rowe and Kennicutt II 2009
DGOMB	S5	2002	Gyre/BC	25.4889	-88.2633	3,312	1		Rowe and Kennicutt II 2009
DGOMB	W2	2000	Gyre/BC	27.4133	-93.3376	625	1		Rowe and Kennicutt II 2009
DGOMB	W3	2000	Gyre/BC	27.1729	-93.3218	860	1		Rowe and Kennicutt II 2009
DGOMB	W5	2000	Gyre/BC	26.2763	-93.3622	2,755	1		Rowe and Kennicutt II 2009
DGOMB	WC12	2000	Gyre/BC	27.3232	-91.5558	1,168	1		Rowe and Kennicutt II 2009
DGOMB	WC5	2000	Gyre/BC	27.7714	-91.7622	400	1		Rowe and Kennicutt II 2009



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The mission of the Bureau of Ocean Energy Management is to manage development of U.S. Outer Continental Shelf energy and mineral resources in an environmentally and economically responsible way.

BOEM Environmental Studies Program

The mission of the Environmental Studies Program is to provide the information needed to predict, assess, and manage impacts from offshore energy and marine mineral exploration, development, and production activities on human, marine, and coastal environments. The proposal, selection, research, review, collaboration, production, and dissemination of each of BOEM's Environmental Studies follows the DOI Code of Scientific and Scholarly Conduct, in support of a culture of scientific and professional integrity, as set out in the DOI Departmental Manual (305 DM 3).