Coral Communities as Indicators of Ecosystem-Level Impacts of the *Deepwater Horizon* Spill

CHARLES R. FISHER, AMANDA W. J. DEMOPOULOS, ERIK E. CORDES, ILIANA B. BAUMS, HELEN K. WHITE, AND JILL R. BOURQUE

The Macondo oil spill released massive quantities of oil and gas from a depth of 1500 meters. Although a buoyant plume carried released hydrocarbons to the sea surface, as much as half stayed in the water column and much of that in the deep sea. After the hydrocarbons reached the surface, weathering processes, burning, and the use of a dispersant caused hydrocarbon-rich marine snow to sink into the deep sea. As a result, this spill had a greater potential to affect deep-sea communities than had any previous spill. Here, we review the literature on impacts on deep-sea communities from the Macondo blowout and provide additional data on sediment hydrocarbon loads and the impacts on sediment infauna in areas with coral communities around the Macondo well. We review the literature on the genetic connectivity of deep-sea species in the Gulf of Mexico and discuss the potential for wider effects on deep Gulf coral communities.

Keywords: aquatic ecosystems, coral reefs, ecology, environmental science

The *Deepwater Horizon* (DWH) rig blowout at the Macondo well site resulted in an oil spill that was fundamentally different from any previous oil spill, because an estimated 4.9 million barrels of oil and gas were released over a period of 87 days from a depth of nearly 1500 meters (m; Peterson et al. 2012, Reddy et al. 2012, and the references therein). The high-temperature mixture of oil and gas was injected into cold seawater at high ambient pressure. The physical processes associated with the conditions of the release coupled with the use of a dispersant at depth led to the production of *microdroplets*, emulsions and dissolved oil and dispersant components (Ryerson et al. 2012 and the references therein). Although buoyant droplets of oil and gas rose to the sea surface, it is estimated that as much as half of all the released hydrocarbons stayed in the water column (FISG 2010, Socolofsky et al. 2011). The existence of a petroleum-hydrocarbon-enriched deep-sea plume was reported by several research teams at depths ranging from 800 to 1200 m (Reddy et al. 2012), and modeling studies indicate that there may have been multiple plumes formed in different density layers (North et al. 2011, Spier et al. 2013). After the oil reached the sea surface, natural weathering processes, burning, and the use of additional aerially applied dispersant resulted in further entrainment of oil into the water column and its subsequent sinking (Passow et al. 2012, Reddy et al. 2012). This deposition of oil onto the seafloor combined with the release of oil and dispersants at depth posed a high risk to deep-sea ecosystems.

The seafloor in the Gulf of Mexico (GOM) is dominated by soft sediments containing diverse communities of meio- and macrofauna. In places where hard bottoms occur, corals, including hard corals (Scleractinia), soft corals (Octocorallia), and black corals (Antipatharia), often colonize this substrate and form the foundation of an associated diverse ecosystem. Here, we review what is known about the effects of the Macondo oil spill on coral and soft-sediment ecosystems in the GOM below a depth of 400 m.

The impact of the Macondo blowout on deep-sea coral communities

Against the background of a sedimented deep-sea floor, current and historical natural oil seepage has contributed to the formation of thousands of discrete areas in which carbonates are exposed in the deep GOM (Fisher et al. 2007, Roberts et al. 2010). Data collected from surface ships, including high-resolution bathymetry and 3-D seismic reflectivity, can indicate likely areas of exposed hard ground on the deep-sea floor (Roberts et al. 2010). On the basis of the interpretation of reflectivity in 3-D seismic data sets, the Bureau of Ocean Energy Management (BOEM) has estimated that there are over 22,000 discrete areas with carbonate deposits within the top 8 m of the seafloor in the northern GOM

*Figure 1. Paramuriceid coral imaged in November 2010 at MC294 with live branch tips, attached floc, and brittle star (**Asteroschema clavigerum**). Reprinted with permission from White and colleagues (2012a).*

visited in the Gulf, in that over half of the corals were partially covered by a brown flocculent material (*floc*), and many colonies exhibited additional signs of stress, including tissue loss and excess mucus production. Evidence that the floc deposition and exhibition of stress had occurred quite recently included the observation of the commensal *Asteroschema clavigerum* ophiuroids, a common occurrence on living paramuriceid corals, still clinging to corals that, in some cases, were completely covered in this floc and were dead or dying (figure 1; White et al. 2012a, 2012b). Samples of the floc were also shown to contain weathered oil with polycyclic aromatic hydrocarbons (PAHs) and hopanoid biomarker ratios consistent with Macondo well oil (White et al. 2012a). These data coupled with the location, depth, and timing of the occurrence and the discovery of this adverse impact implicated the Macondo blowout as the likely causative factor in the damage to the deep-sea corals at MC294. A simple calculation based on the age of the corals (mean $[M]$ = 507 years, standard deviation $[SD]$ = 58; Prouty et al. 2014) and the lack of any similar evidence of impacts at 20 other deepwater coral sites in other parts of the GOM investigated in the same time frame after the spill yielded a probability of the adverse impact on corals happening coincidently at this time and place of approximately .0001 (White et al. 2012b).

(*http://io.aibs.org/boem*). However, this data set does not discriminate between buried carbonates and those exposed on the seafloor. Visual examination is required to confirm the presence of exposed hard ground and of any associated biological communities. As a result, our direct knowledge of the occurrence, composition, and distribution of coral communities in the deep GOM is quite limited, although recently developed predictive models may improve our ability to locate coral communities in the deep Gulf (Georgian et al. 2014).

In late 2010, as part of a deliberate effort to locate a coral community in the vicinity of the spill site, a coral community was discovered in BOEM lease block MC294, 13 kilometers (km) to the southwest of the Macondo wellhead (White et al. 2012a). It was apparent that this community was different from any other deep-sea coral community that had been previously

In a follow-up study, Hsing and colleagues (2013) tracked changes in the condition of individual corals from the MC294 site, using high-resolution images obtained during five visits to this site over 16 months (figure 2). A reduction in the average level of apparent impact over this time period was
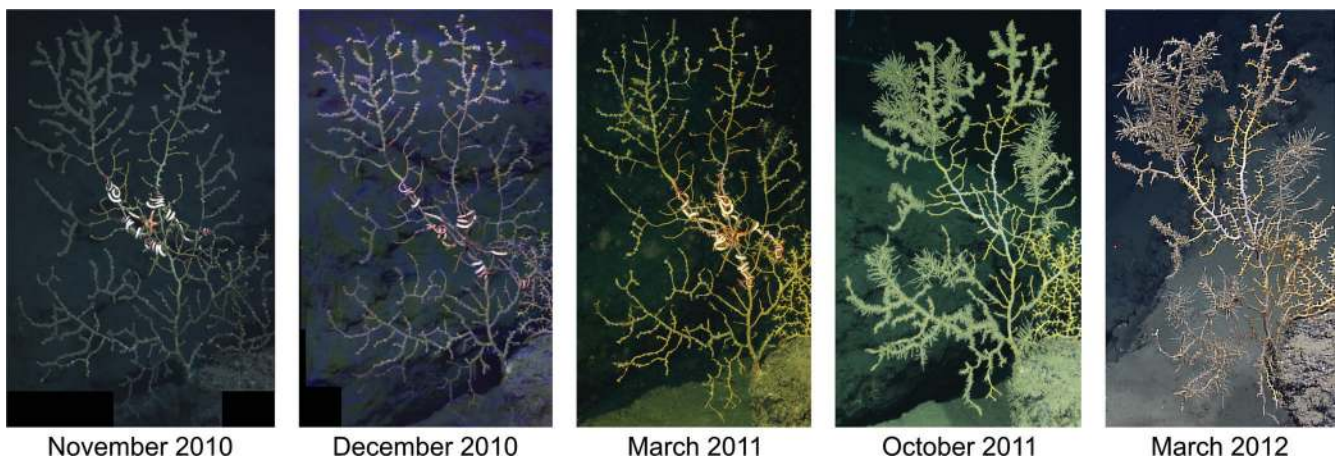

November 2010   December 2010   March 2011   October 2011   March 2012

*Figure 2. Progression of the impact on a **Paramuricea biscaya** colony at MC294 between November 2010 and March 2012. Most of the adherant floc present in 2010 had fallen off by March 2011. The patchy hydroid growth first apparent in March 2011 is extensive by October 2011 and continues through March 2012, when terminal branch loss becomes apparent. Reprinted with permission from Hsing and colleagues (2013).*
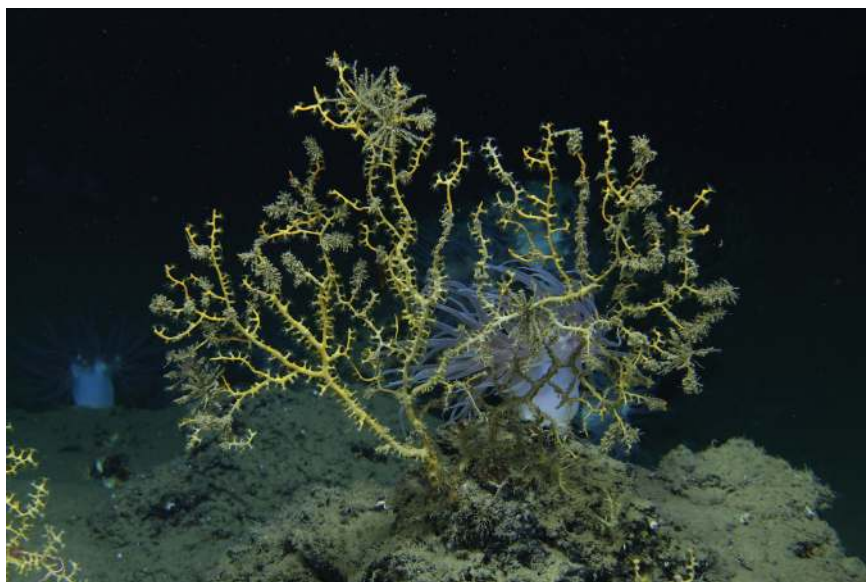
Figure 3. **Paramuricea biscaya** *colony in November 2012 at MC297 with the patchy hydroid covering characteristic of corals affected by the Macondo spill. Photographs: Charles R. Fisher.*

found and attributed to a decrease in the surface area of corals covered by floc. Furthermore, colonies observed with low levels of floc on their surface in 2010 (less than 20% coverage) were likely to exhibit apparently complete recovery of the floc-covered branches by March 2012. However, the degree of initial visible impact was significantly correlated with lasting damage and secondary colonization by hydroids by March 2012. These data indicate that the effect on the coral colony is cumulative and not a simple reflection of the response of individual polyps or branches to the exposure (Hsing et al. 2013).

Hsing and colleagues (2013) also found that the impact and subsequent response were patchy on several spatial scales. Not only was the level of visually apparent impact on adjacent corals often very different but so, too, was the impact within a coral colony. As a result, hydroids exhibited a patchy distribution on moderately affected corals by March 2012, with apparently healthy branches intermingled with the dead portions of branches heavily colonized by hydroids. The appearance of these corals was very distinctive (figure 3) and proved to be a powerful diagnostic tool for recognizing other corals affected in a similar way and during a similar period but not discovered until after the original floc on the corals was no longer present.

To determine whether there were additional coral communities in the vicinity of the Macondo wellhead, two cruises using towed cameras and autonomous underwater vehicles were used to explore the seafloor. These surveys resulted in the identification of five previously unknown discrete sites hosting colonial corals within 30 km of the Macondo wellhead (Fisher et al. 2014). The corals at each newly discovered site were then surveyed using a remotely operated vehicle (ROV) for evidence of recent deleterious impact.

Two newly discovered communities, one (MC297) located 6 km south of the Macondo wellhead and 13 km from the site in MC294 and another (MC344) 22 km southeast of the Macondo wellhead, were determined to host coral communities that had also been affected by the spill. At the MC297 site, a total of 69 octocoral colonies present in two localized areas and separated by approximately 370 m were imaged. Of the 69 colonies imaged, 47 exhibited the characteristic patchy hydroid colonization pattern on at least 5% of the colony, and two others had no living tissue. The death of these two corals was attributed to the Macondo blowout, because they had died recently enough to still retain small dead branches. The number of colonies affected in the coral communities at MC294 and MC297 were similar (72% and 68%, respectively), although 16% of the corals at MC297 showed signs of impact on over 50% of the colony, compared with 8% in this condition at MC294 at this point in time (Fisher et al. 2014). The coral community in MC344 at a depth of 1875 m exhibited a smaller but notable level of impact that was still apparent in October 2011. At this site, 23% of the 30 corals imaged showed evidence of impact on more than 5% of their colony, but none showed an impact on over 50% of the colony. This site is notable because of the distance from the spill and the fact that it is even farther below the depths at which deepwater hydrocarbon plumes that formed during the spill were reported (Reddy et al. 2012 and the references therein).

Sediment cores can reveal the history of oil contamination at a site and can help distinguish recent deposition from ongoing natural oil seepage, which would result in relatively elevated oil levels throughout the top 10 centimeters (cm) of a core, whereas recent deposition of oil would result in higher oil concentrations in the upper 1 cm relative to the deeper strata. Somewhat elevated oil concentrations in sediments are expected in proximity to deepwater coral communities, because the carbonates on which corals are normally found in the deep GOM (Fisher et al. 2007, Cordes et al. 2008) form in areas with current or historical seepage (Roberts et al., 2010). In fact, most sediments collected in the deep GOM contain some oil, which reflects basin-wide and atmospheric inputs (e.g., Sassen et al. 1994).

Oil content was examined in sediments collected at 10 sites associated with deepwater coral communities located between 6 and 194 km from the Macondo wellhead (figure 4). The top 0–1 cm and 5–10 cm sections of the sediment cores were analyzed for the total amount of saturated hydrocarbons and PAHs by Alpha Analytical Laboratories, and the data are available at *www.gulfspillrestoration.noaa. gov/oil-spill/gulf-spill-data* (for detailed methods, see the
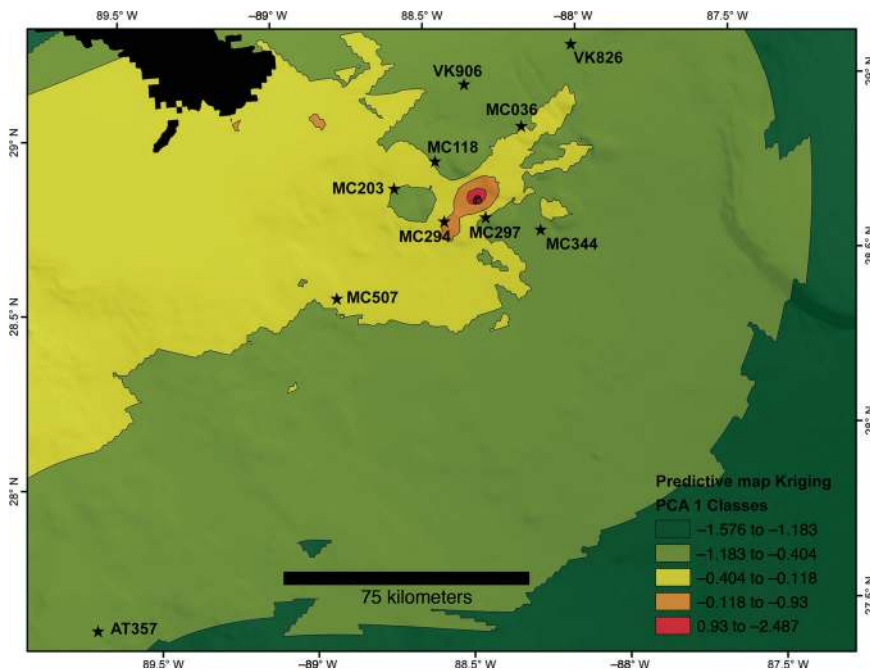
Figure 4. The region around the Macondo well, showing bathymetry; the coral sites investigated for recent impact; and the interpolated area of impact on sediment infauna reported by Montagna and colleagues (2013). The interpolation was based on a principal components analysis (PCA) of several correlated biological and chemical variables, including polycyclic aromatic hydrocarbon concentrations and the composition of the sediment communities. Source: Adapted from Montagna and colleagues (2013).

colleagues (2014) concluded that corals at this site exhibited less-severe but notable visual evidence of an impact from the Macondo blowout, consistent with the elevated surface hydrocarbon concentrations in the surrounding sediments. This site, like the other MC sites and AT357, has active seep areas in the vicinity of the corals, which are reflected in sometimes-elevated levels of hydrocarbons in deeper core strata (figure 5, table S1).

AT357 is located almost 200 km from the Macondo wellhead and, because no impact on the corals at this site was evident, it was used as a reference site by Fisher and colleagues (2014). When hydrocarbon data from both deep and shallow strata of the cores at this site were considered, it was clear that there was ongoing active seepage at AT357, but there was no evidence of recent hydrocarbon deposition to surface sediments. Similarly, at MC118, the relatively high total saturated hydrocarbon and PAH concentrations in the deeper strata of the sediment cores are consistent with the very active seepage at this well-studied site (Lapham et al. 2008), and similar levels in surface sediments suggest little new surface deposition in the areas we sampled at this site only 18 km to the north of the Macondo wellhead.

supplemental material). Most cores from sites less than 30 km from the Macondo wellhead, including cores from MC294, MC297, and MC203 and the core taken from MC344 in 2010, had significantly higher levels of total saturated hydrocarbons and PAHs in the surface sediments than deeper in the cores (figure 5). The concentrations of hydrocarbons in the surface fractions were an order of magnitude higher than those in the deeper fractions for all of these sites except MC344. These data indicate recent deposition of oil at higher levels than had occurred from historical seepage. The average total saturated hydrocarbon concentrations within the top 1 cm were much higher at MC294 and MC297 than at any other sites, and the concentrations in the lower 5–10-cm sections were in the same range or lower than those from other sites (figure 5, supplemental table S1). The PAH concentrations in the top 1 cm of the cores taken from MC294 and MC297 were within the range documented in the Operational Science Team (OSAT) report for samples taken from within 3 km of the wellhead (OSAT 2010) and in the high-impact zone-1 area defined by Montagna and colleagues (2013). These data provide further direct evidence that the impact on the corals at MC294 and MC297 was from a recent and anomalous event that deposited significant oil on the seafloor over a wide area.

MC344 had the next highest total saturated hydrocarbon concentrations in the top 1 cm of the cores. Fisher and

The impact of the Macondo blowout on soft-sediment communities

Most of the deep-sea floor is covered by soft sediment, which harbors a highly diverse fauna (Hessler and Sanders 1967, Rex and Etter 2010) that is important to ecosystem health and functioning (Danovaro et al. 2008). Benthic infauna are sensitive indicators of environmental change to their sediment habitat, including abrupt impacts such as oil spills. Infauna perform a suite of ecological functions, including nutrient cycling and bioturbation, as well as serving as food resources for higher trophic levels. The two primary community groups present in deep-sea sediments are operationally defined as the *meiofauna* (between 45 and 300 micrometers [μm]) and macrofauna (larger than 300 μm). In addition to the size differences, these faunal groups are dominated by different phylogenetic taxa. Meiofauna are dominated by nematodes and harpacticoid copepods, and macrofauna are dominated by polychaete annelids, peracarid crustaceans, and mollusks. Crustaceans, such as amphipods and harpacticoid copepods, are particularly sensitive to oil and other environmental contamination (Raffaelli and Mason 1981, Peterson et al. 1996), and reductions in their density can be used as indicators of contamination. In contrast,
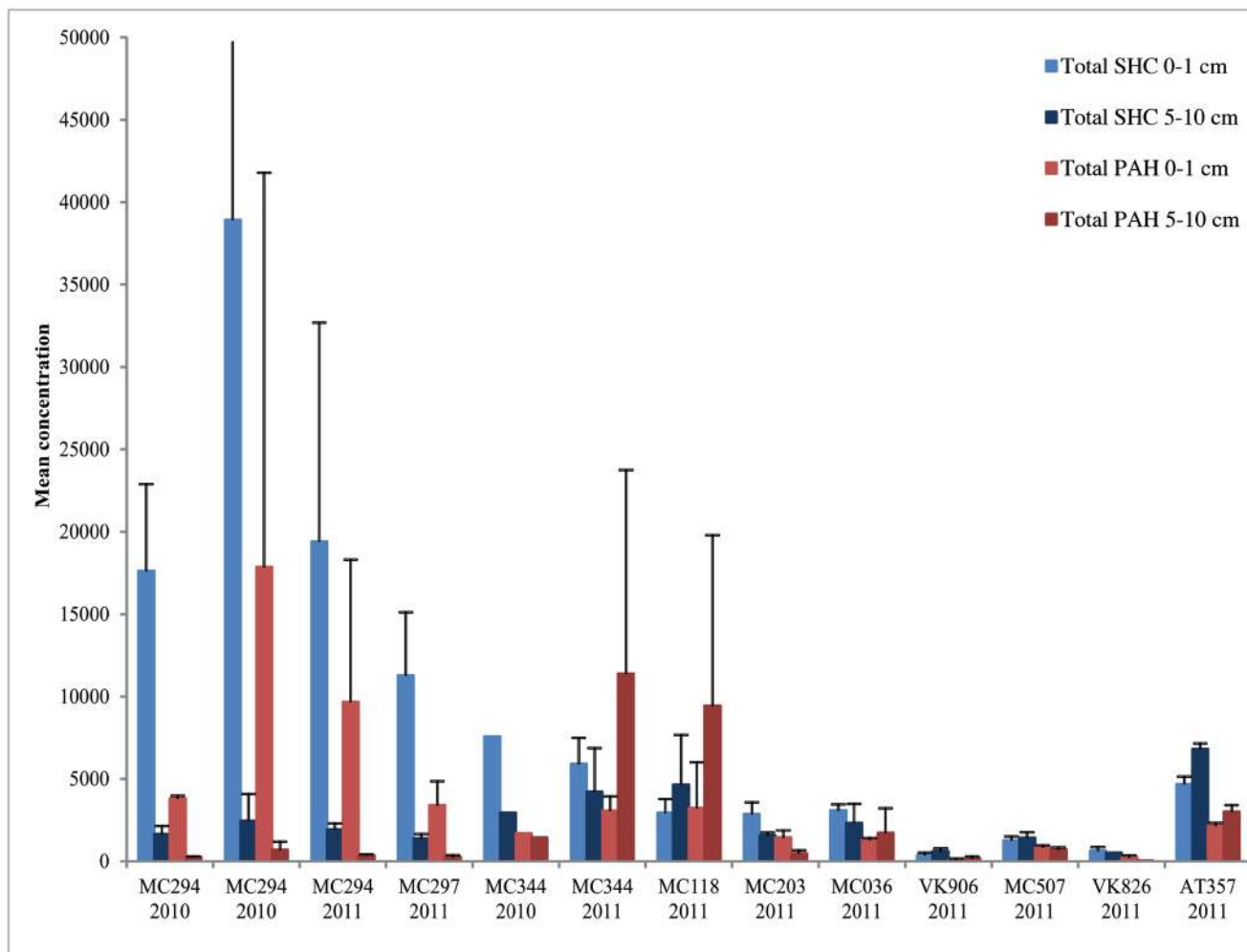
Figure 5. The average total saturated hydrocarbons (SHC) and total polycyclic aromatic hydrocarbon (PAH) concentrations (in micrograms per kilogram [µg/kg]) from sediment samples collected in 2010 and 2011 from the Gulf of Mexico. The top fraction (0–1 centimeter [cm]) and bottom fraction (5–10 cm) of sediment cores were sampled. The error bars represent the positive standard deviation (S.D.). The error bar for MC294 2010 extends to 82,874 µg/kg. Source: All data were taken from the National Oceanic and Atmospheric Administration's Natural Resource Damage Assessment Web site (www.gulfspillrestoration.noaa.gov/oil-spill/gulf-spill-data).

most polychaete and nematode species are more tolerant of oil, and there are species with opportunistic life histories and feeding strategies that allow them to capitalize on the organic enrichment associated with events such as oil spills. Therefore, these taxa have been found to increase in density following such events (Peterson et al. 1996). These varied responses typically result in an overall reduction in diversity and median body size and an increase in density leading to a numerical dominance of opportunistic species with broad environmental tolerances (Gage 2001). As a result, the abundances of higher taxonomic groups and changes in the abundances of specific species can be used as robust indicators of anthropogenic impacts on the deep-sea benthos.

To examine the footprint of oil deposited on the seafloor from the Macondo blowout, an extensive sediment-sampling program was initiated in September 2010, 2 months after the wellhead was capped. Of the 115 sediment samples collected from the deep sea (OSAT 2010), 29% showed a potential indication of contamination by oil, and 6% exceeded the aquatic life benchmark values for oil-related compounds (USEPA 2003, 2008) and were considered likely toxic to aquatic organisms (OSAT 2010). All samples reported in OSAT (2010) that exceeded an aquatic life benchmark ratio of 1 were collected within 3 km of the wellhead, and only sediments collected within 3 km of the wellhead had oil that was unambiguously identified as oil from the DWH spill by OSAT in 2010. The total PAH concentrations in sediments sampled within this 3-km zone ranged from 9900 to 28,000 micrograms per kilogram [µg/kg]—considerably higher than concentrations found in sediment cores collected before the spill by Rowe and Kennicutt (2009; 0–1030 µg/kg) and in a prior study of the relationship between sediment

oil content and the proximity to oil rigs (94–748 µg/kg in samples taken away from rigs; CSA 2006).

In order to assess and map the footprint of the impact on the soft-sediment fauna in the deep sea, Montagna and colleagues (2013) sampled in a radial pattern at discrete distances from the wellhead, using a sediment multicorer. Montagna and colleagues (2013) outlined zones of impact on a scale of 1 (highest) to 5 (lowest) based on a principal components analysis of several correlated biological and chemical variables, including PAH concentrations and the composition of the sediment communities. The PAH concentrations in zone 1 ranged from 459 to 47,600 µg/kg. However, concentrations of PAHs and total petroleum hydrocarbons in surface sediments (0–3 cm) were patchy throughout the region. Overall, PAH content was negatively correlated with macrofaunal and meiofaunal diversity and positively correlated with nematode:copepod ratios (Montagna et al. 2013).

Montagna and colleagues (2013) derived an interpolated map of levels of the impact on deep benthic communities from the principal components analysis (figure 4). They estimated the extent of the high-impact area as approximately 24.4 square kilometers (km²) and moderate-impact areas as an additional 148.3 km². Although there was a high density of sampling within 3 km of the wellhead, fewer soft-sediment stations were sampled beyond 3 km. These maps present a robust regional view of the impact on sediment communities from the oil spill, however details must be interpreted with caution in areas with lower sampling densities, especially because seafloor deposition of oil may be quite patchy.

Impact on soft-sediment communities associated with corals.

The Montagna and colleagues (2013) maps were based on sampling of soft sediments. However, the deposition of particulate matter in the deep ocean, including substances such as low density marine oil-snow, will be favored in areas where there are depressions and low near-bottom current velocities (Nowell and Jumars 1984). Corals, however, favor areas of the seafloor with sufficient currents to facilitate food delivery and gas exchange (Dorschel et al. 2007, Georgian et al. 2014), and therefore, a deepwater coral community could be significantly affected by hydrocarbons, dispersants, or other potential toxicants suspended or dissolved in near-bottom water, in a habitat that is not conducive to sediment deposition and accumulation.

Although Montagna and colleagues (2013) analyzed the effects of the spill on the background soft-sediment communities, the response of infaunal communities associated with deep-sea coral communities was not included in their analysis. Here, we summarize new data on coral-associated infaunal communities from affected and unaffected deepwater coral sites. Sediment cores (6.35 cm in diameter, 10 cm deep) were collected in 2010 within lease block MC294 adjacent to coral colonies; three sets of cores were collected near *Paramuricea biscaya* colonies at the affected coral site

described by White and colleagues (2012a) and one set near a *Madrepora oculata* colony about 400 m away (supplemental tables S2a and S2b). Sediments near *P. biscaya* at the White and colleagues (2012a) site were resampled in 2011, along with sediments near corals located 59 km (MC507; depth, 1043 m) and 194 km (AT357; depth, 1048 m) from the wellhead (figure 4). These sites are dominated by the same coral genera as MC294 (Doughty et al. 2014) and, given their distance from the wellhead, their lack of visible acute damage from the spill (Fisher et al. 2014) and their lack of an enriched hydrocarbon signal in surface sediments (figure 5), are used as reference sites for the purposes of infauna evaluation. Infaunal macrofauna were quantified and identified at a family level and meiofauna at the order level or lower, and community metrics, including diversity, abundance, and community composition, were determined.

Deep-sea corals alter local flow patterns, can increase available organic matter, and provide shelter for a variety of consumers (Raes and Vanreusel 2005); all of these factors can influence the composition and diversity of sediment macro- and meiofauna in the vicinity of deep-sea corals. We found that the sediment macrofaunal communities associated with deep-sea corals differed from those in background sediments in several significant ways. Infaunal community structure in coral-associated sediments at MC507 and AT357, two coral sites not affected by the DWH spill, was significantly different from that of communities found in the background soft sediments of similar depth ranges (Rowe and Kennicutt 2009, Wei et al. 2010), determined on the basis of nonmetric multidimensional scaling and an analysis of similarities (ANOSIM) of square-root transformed abundance data (ANOSIM $R > .99$, $p < .025$; figure 6). Polychaetes dominated all coral habitats sampled at MC294 and MC507 and represented a higher proportion of the community (70%–95%) than the community associated with background soft sediments (50%; figure 7), which contained a higher proportion of crustaceans and other taxa. Evenness was generally lower but was highly variable at coral sites close to the wellhead relative to the rest of the GOM (Wei et al. 2010). It follows that the level of *taxa dominance*, communities characterized by a high abundance of few taxa, was higher among all the deep-sea coral communities than those of the background soft sediments (supplemental figure S1). Although macrofaunal densities were higher near corals, meiofaunal densities in coral-associated sediments were significantly lower ($p < .05$) than those found in background prespill soft sediments (Baguley et al. 2006, Rowe and Kennicutt 2009) and were not significantly different ($p > .05$) from low-impact zones sampled after the spill (Montagna et al. 2013). Meiofaunal diversity and evenness at all of the coral habitats in 2011 were comparable to those in lower-impact zones 3, 4, and 5, sampled in 2010 (supplemental table S2c; Montagna et al. 2013). The nematode:copepod ratio was lower at all of the sampled coral sites, except one (MC294-2010), and were similar to the GOM mean ($M = 5.7$, SD = 1.8; Baguley et al. 2006). Although soft-sediment meiofaunal communities in
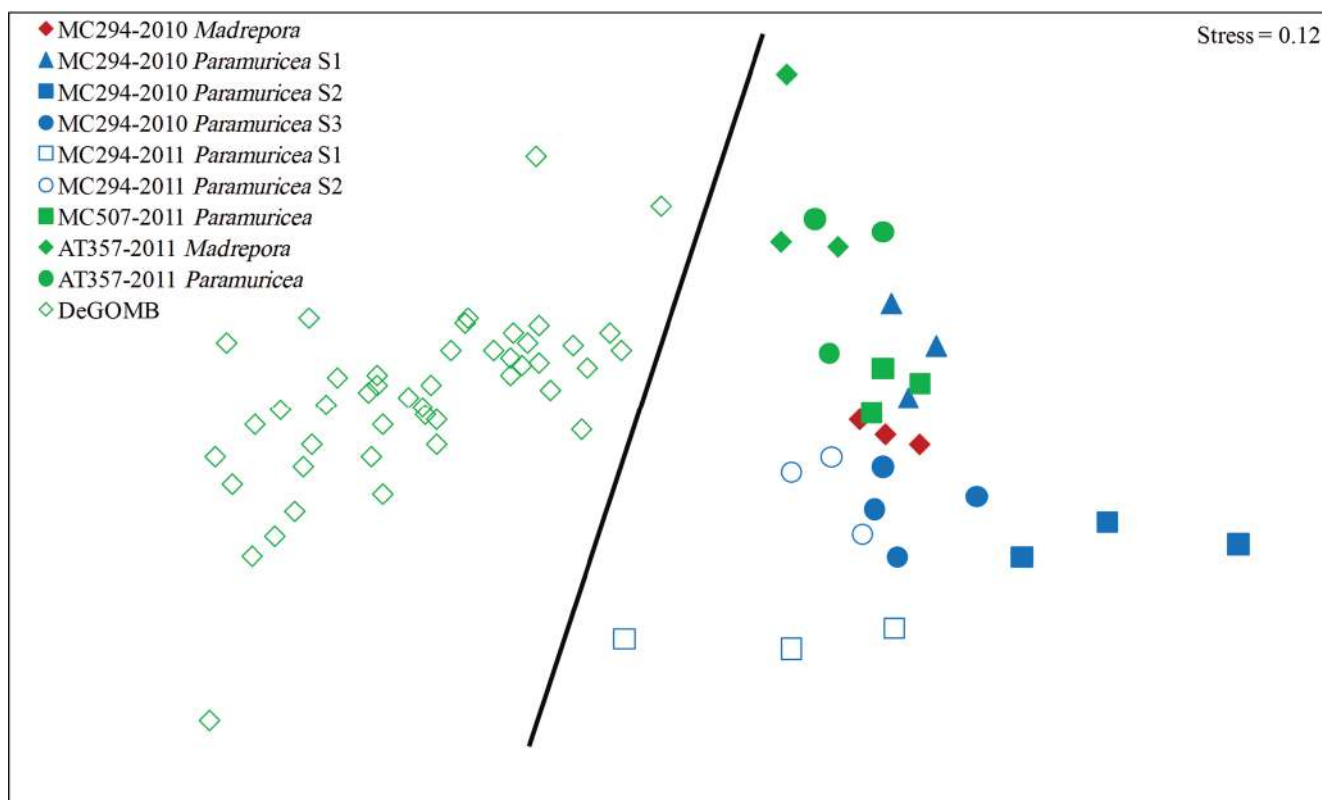
Figure 6. Nonmetric multidimensional scaling results of macrofaunal assemblages from stations of the Deep Gulf of Mexico Benthos Program (DeGOMB; Rowe and Kennicutt 2009, Wei et al. 2010) and deep-sea coral habitats in 2010 and 2011, based on Bray–Curtis similarities of square-root transformed abundance data. The illustrative line represents a similarity of 21%.
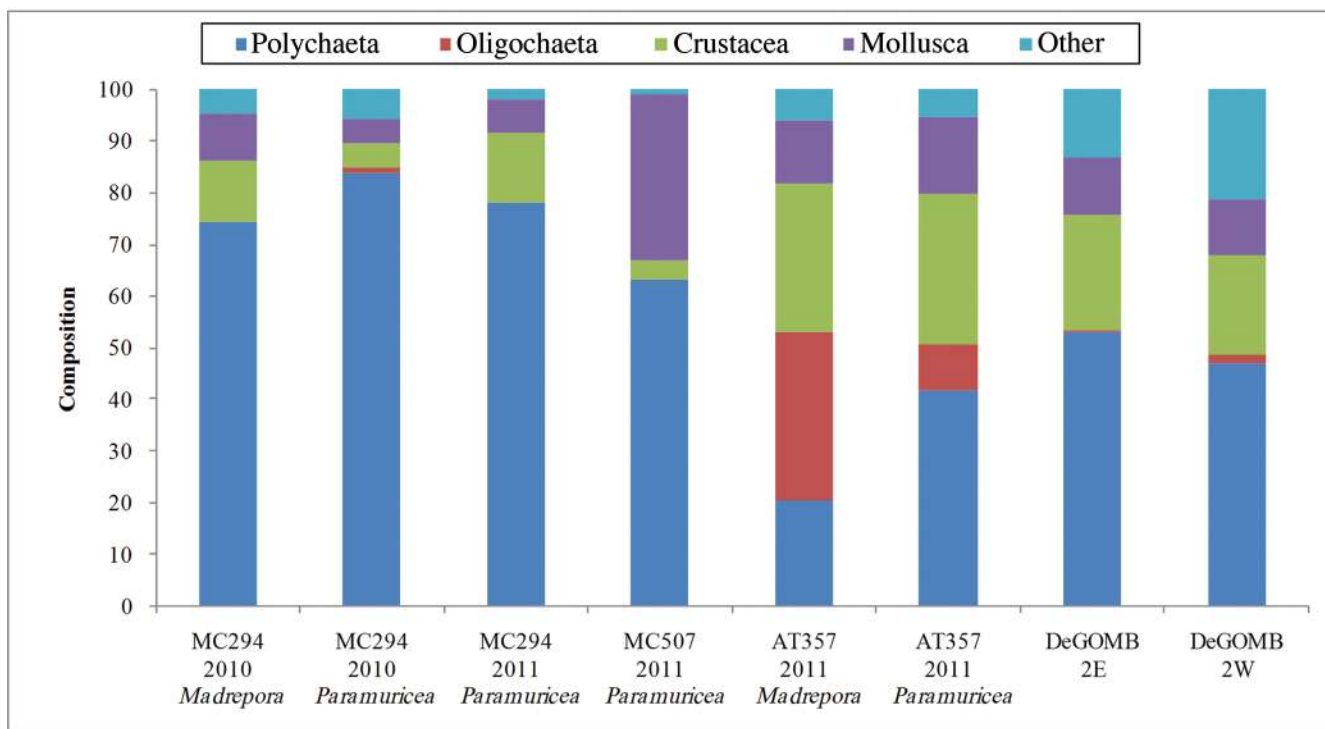

Figure 7. Percentage of taxa composition based on the mean macrofaunal densities of major taxonomic groups from all sites with appropriate data available. Abbreviations: DeGOMB, the Deep Gulf of Mexico Benthos Program; 2E and 2W, DeGOMB-designated zones.

the GOM are typically structured by surface productivity, with declines in density with increasing depth (Baguley et al. 2006), meiofaunal communities associated with deep-sea corals differ because of localized accumulation of organic matter and differences in sediment granulometry (Vanreusel et al. 2010). This may explain why coral-associated sediment communities do not appear to respond to oil contamination in the same way as soft-sediment communities do.

There was a clear indication of an impact from the Macondo blowout on the macrofaunal infauna communities at MC294 when that site was compared with reference locations at AT357 and MC507. The infaunal communities at MC294 were significantly different from the communities at MC507 and AT357 on the basis of the ANOSIM (2011, $R > .46$, $p < .03$). The sediment communities at the reference site (AT357) had higher proportions of crustaceans than the affected site (MC294; figure 7), similar to background soft sediments at comparable depths (e.g., sites in the Deep Gulf of Mexico Benthos Program; Rowe and Kennicutt 2009, Wei et al. 2010). The sediments at MC507 had a greater proportion of mollusks than those at MC294. High variability in macrofaunal densities was evident among *Paramuricea* habitats sampled at MC294 (table 2a–2c), which is consistent with the high variance observed in sediment oil concentrations. In addition, macrofaunal diversity at MC294 site 1 was significantly lower than that within *Paramuricea* habitats at AT357 ($p = .003$).

As was observed for the corals, changes in the infaunal communities were observed over time following the initial impact. Between 2010 and 2011, the polychaete community dominants shifted at MC294; the proportion of dorvilleid polychaetes decreased, whereas paraonids increased (supplemental figure S2). Other polychaete families that dominated in 2010 included Capitellidae and Cirratulidae, both of which are known to be opportunistic taxa (Pearson and Rosenberg 1978) that are often used as indicators of oil contamination (Davies et al. 1984). Representative species in the family Capitellidae are capable of dominating disturbed, organically enriched sediments by exploiting the lack of competition and by rapidly reproducing (Gray et al. 1979). Certain species of cirratulids are able to tolerate some level of oil contamination but are unable to reproduce in order to rapidly colonize disturbed habitats (Gray et al. 1979). Particular dorvilleid species are commonly found in extreme environments, including heavily polluted sediments, seeps, and oxygen minimum zones (Fauchald and Jumars 1979, Levin 2005). In contrast, amphipod crustaceans that are sensitive to oil contamination were present at most stations in 2010 but were absent in 2011 at MC294. These changes are consistent with an initial hydrocarbon loading during the spill, which was followed by a subsequent decrease in total organic content over time. Macrofaunal densities declined at MC294 in 2011, potentially as a function of multiple factors, including decreased organic matter available for food, increased predation, and a delayed response from the impact of the oil spill, as was reported by Sanders and colleagues (1980) following an oil spill off the coast of Massachusetts.

Monitoring these fauna over time will facilitate our understanding of the timescales involved for impact and recovery.

Temporal patterns observed for meiofaunal communities at the affected coral site were similar to those in the macrofauna, with a decrease in overall densities between 2010 and 2011 (table S2b). A change in the abundance of nematodes and copepods at MC294 from 2010 to 2011 was observed, with nematode densities declining and copepod densities increasing. This change in the nematode:copepod ratio is consistent with previously reported responses to high organic loading (Raffaelli 1987). At one location in MC294, meiofaunal densities were an order of magnitude higher in 2010 than in 2011, which potentially represents rapid recruitment or colonization of meiofaunal benthos in response to oil loading of the sediments. Although changes in meiofaunal densities and composition between 2010 and 2011 were evident, we have yet to see what long-term changes may occur within the coral-associated sediment communities.

A microscopic examination of sediments from MC294 indicated the presence of meiofauna and small unusual particles that had not previously been observed in deep-sea sediments (examples are shown in figure 8). These particles, which were tens of microns in diameter, were atypical because of their dark brown coloring and the presence of small, 1-mm-diameter orange spheres. Because of their irregular appearance, 20 samples including meiofauna (3 nematodes and 1 gastropod; figure 8a) and particles (16 total, including those shown in figure 8b–8f and other similar particles) were isolated from sediment cores and examined for oil using a gas chromatograph coupled to a flame ionization detector. Oil was observed in all particles as *n*-alkanes, with a carbon preference index of 0.95–1.05 and as an unresolved complex mixture. The presence of *n*-alkanes ranging from C_{16} to C_{38}, with C_{21} as the most abundant *n*-alkane, is indicative of oil that is less weathered than oil from natural seepage, which is depleted in *n*-alkanes (Sassen et al. 1994). Therefore, it is likely that the oil in the meiofauna and particles had been recently deposited in the sediments and is from the Macondo well. These 20 subsamples had average oil concentrations of 55,600 µg per gram (g)—three orders of magnitude greater than the sediments from which they were taken (17.6 mg/g; table S1). The nematode samples had the highest oil concentrations (314,000 µg/g), and, although the detritus samples had the lowest (143–20,300 µg/g), these concentrations were still at least one order of magnitude greater than the sediment from which they were taken. Although the amounts of oil in these small samples were too low to determine the source of the oil from biomarker ratios, it is evident that infauna were exposed to sediment subfractions with high oil contents unlikely to have been derived from natural seepage.

The potential impact on communities outside of the acute-impact footprint

Although the evidence for acute impact is limited to the sites that we could discover and characterize, it is likely
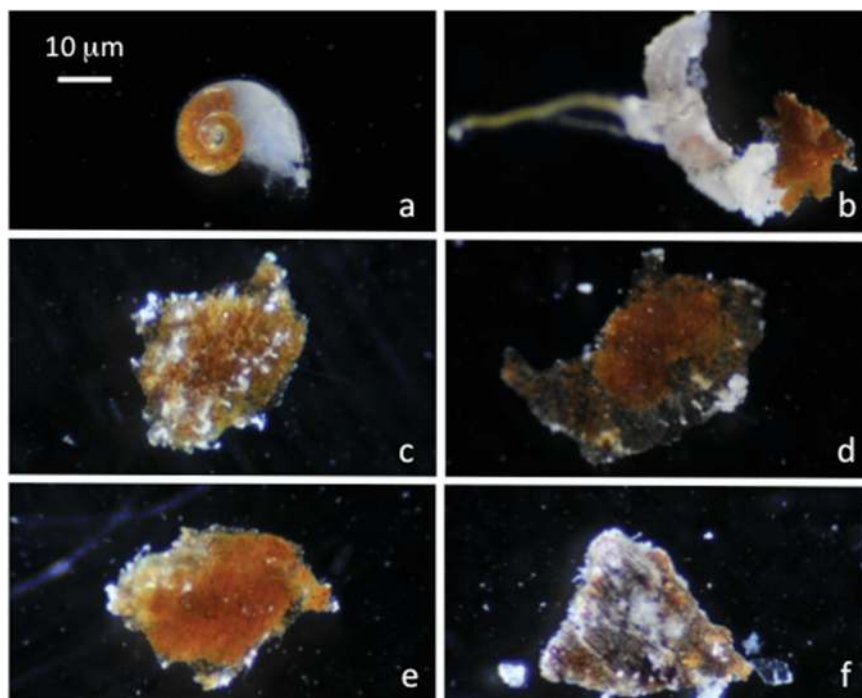
Figure 8. Microscopic images of a gastropod containing internal orange spheres (a) and unusual particles (b–f) collected from MC294. Micrographs: Erik E. Cordes.

Existing data from deep-sea organisms indicate that many grow slowly, mature late, and achieve old age with low energetic investment in sexual reproduction relative to shallow-water organisms (Sanders 1979). For example, some colonies of the black coral *Leiopathes glaberrima* are estimated to be 4000 years old (Roark et al. 2006). Paramuriceids are also very long lived; in fact, some specimens from sites affected by the Macondo blowout are over 500 years old (Prouty et al. 2014). Because of the presumed limited energetic investment in sexual reproduction, the rate of sexual recruitment should also be low (Young C 2003). The *Paramuricea* species affected in the spill exhibited size–frequency distributions that suggested very low recruitment rates, with high mortality of new recruits (Doughty et al. 2014). Other indirect evaluations similarly indicate that sexual recruitment is low and periodic in deepwater solitary corals (1 in 25 years; Thresher et al. 2011) and slow and associated with high mortality rates in octocorals (Grigg 1988). The limited number of studies in which a direct measurement of sexual recruitment rates was conducted also showed low successful sexual recruitment in many but not all deep-sea corals. Lacharité and Metaxas (2013) found high rates of recruitment for a broadcast spawning octocoral (*Primnoa resedaeformis*), whereas sexual recruitment rates for the brooding octocoral *Paragorgia arborea* were about a thousandfold lower on experimental settlement tiles deployed over a 4-year period. Mortality rates of recent recruits were high, even for the species with higher recruitment rates (Lacharité and Metaxas 2013).

Low sexual recruitment rates of deep-sea coral populations make these species vulnerable to local extirpation when adult populations are diminished. External sources of larvae then become important in the recovery of locally devastated populations. The antipatharian *L. glaberrima* shows genetic differentiation between colonies offshore of Louisiana and Alabama and sites farther southeast, off the coast of southern Florida and to the west of the Mississippi Canyon, which indicates limits to gene flow among sites and, therefore, limited potential for recolonization of locally affected sites from other sources (Ruiz-Ramos et al. 2014). Strong depth zonation is apparent in the overall composition of the octocoral communities of the deep GOM, which suggests that depth, rather than distance, is the most significant factor affecting gene flow in this group (Quattrini et al. 2013). The largest known *P. biscaya* populations are found at the deeper (2400–2600 m) sites on the northern end of the Florida Escarpment (Doughty et al. 2014), but gene flow to the shallower (1300–1900 m) impact sites may be rare.

that there are other hard-ground sites that were exposed to deepwater plumes, sinking oil residues from surface burning, or oil and dispersant contained in marine snow. More important, the studies reviewed above only characterize the visually obvious and acute impact on the corals and changes in infaunal communities. There are likely to be invisible impacts, including long-term, sublethal impacts to fauna, either directly on reproductive tissue or, more generally, from the energetic cost of dealing with toxicant exposure. The toxicity of oil and dispersant to deep-sea corals has been confirmed in laboratory experiments with adult colonies. Oil, dispersant, and oil–dispersant mixtures caused partial or total fragment mortality in two octocoral and one antipatharian (black coral) species from the deep GOM (Ruiz-Ramos et al. 2014, Young DM and Cordes 2014). Effective wound healing from partial mortality events caused by oil or dispersant exposure will be important to the fitness of the colonies (Fong and Lirman 1995). However, wound healing and other responses to toxicant exposure divert energy from sexual reproduction, presumed to be already low in deep-sea corals. The results from work on shallow-water corals indicate that oil or dispersant exposure causes direct disruptions to the reproductive cycle, ranging from the release of premature or less-healthy larvae to the alteration of larval swimming and settlement behavior (Epstein et al. 2000, Goodbody-Gringley et al. 2013). These types of chronic adverse effects are not immediately visible but may have long-term impacts on coral communities in the deep GOM.

Although it is important to determine which populations exchange migrants often enough to prevent genetic differentiation, one must also consider the number of larvae exchanged among sites over the more ecologically relevant timescale of a few years (Cowen et al. 2006). Advances in coupled biophysical dispersal models have made such estimates possible (Cowen et al. 2006). In these models, particles are endowed with certain characteristics related to the life history of the species in question, such as spawning times, time spent in the water column, vertical migration behavior, and the time to reaching a suitable settlement substrate. By tracking the dispersal of these particles, the number of larvae exchanged among sites can be constrained at more ecologically relevant timescales. Early results indicate that only tens of virtual coral larvae successfully disperse between the Vioska Knoll and Garden Banks each year (Baums et al. 2014). The low number of successfully dispersing particles, together with presumed high postsettlement mortality as observed in most deep-sea coral species, including *P. biscaya* (Doughty et al. 2014), is consistent with low connectivity estimates from the genetic data for *L. glaberrima* (Ruiz-Ramos et al. 2014).

Corals as deep sentinels.

The northern GOM region remains the largest oil-producing province in the continental United States. Demand for domestic oil is unlikely to diminish in the foreseeable future, and exploration and production will continue in deeper and deeper waters as technology allows (USEIA 2014). At the same time, the GOM is exposed to other environmental stressors, including high fishing pressure; ocean acidification; and runoff from the Mississippi River that delivers excess nutrients, organic loading, and other pollutants to the region. Deep benthic ecosystems may inevitably be affected by these ongoing anthropogenic activities, and colonial corals are proving to be reliable indicators of both mechanical disturbance and water-borne toxicants in the deep sea. Octocorals—the taxa Calcaxonia, Holaxonia, and Scleraxonia in particular—have a morphology and life history that is well suited to visual monitoring programs. They are normally quite long lived (Prouty et al. 2014) and are covered with polyps and living tissue over nearly 100% of their skeleton. The slow growth with an upright and often planar growth form facilitates repeated imaging and the detection of changes in the colonies (Hsing et al. 2013). Furthermore, they derive food and exchange metabolic gases across tissues directly exposed to epibenthic water. As a result, these corals interact directly with toxicants dissolved in water or incorporated in food sources or other particulates. Because they are attached, damaged, or killed, colonies remain in place, providing a record of deleterious impact even if the affecting agent does not deposit residues on the seafloor (Fisher et al. 2014). Furthermore, because colonial corals are largely limited to carbonates and humanmade structures in the deep GOM, they are likely to be present in most oil-producing regions (Fisher et al. 2007). Coral-monitoring sites throughout the deep GOM have the potential to serve as the proverbial canaries in the coal mine and can provide critical data on the health of the GOM benthos in the coming years.

Supplemental material
The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu129/-/DC1*.

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Charles R. Fisher (cfisher@psu.edu) and Iliana B. Baums are affiliated with the Biology Department at Pennsylvania State University, in University Park. Amanda W. J. Demopoulos is affiliated with the US Geological Survey (USGS) Southeast Ecological Science Center, in Gainesville, Florida. Erik E. Cordes is affiliated with the Department of Biology at Temple University, in Philadelphia, Pennsylvania. Helen K. White is affiliated with the Department of Chemistry at Haverford College, in Haverford, Pennsylvania. Jill R. Bourque is affiliated with Cherokee Nation Technology Solutions, contracted to the USGS Southeast Ecological Science Center.