How Did the Deepwater Horizon Oil Spill Impact Deep-Sea Ecosystems?

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(top) *Anoplogaster cornuta* (fangtooth fish, mesopelagic). (middle) *Gigantura chunni* (telescope fish, mesopelagic and bathypelagic). (bottom) Larval Exocoetidae (flying fish, epipelagic). *Photos courtesy of Danté Fenolio, DEEPEND Consortium*

ABSTRACT. Approximately 90% of the volume of the Gulf of Mexico is contained in water deeper than 200 m, a region where the Deepwater Horizon (DWH) blowout had more impact on ecosystems than any previous oil spill. The remoteness and relative inaccessibility of the deep sea makes documenting even acute impacts to the animals that live in this realm difficult. This article reviews Natural Resource Damage Assessment studies and follow-up work funded as part of the Gulf of Mexico Research Initiative that targeted deepwater pelagic and benthic fauna. Oil was incorporated into the pelagic food web, and a reduction in planktonic grazers led to phytoplankton blooms. Fish larvae were killed, and a generation may have been lost. Cetaceans were killed, and many avoided the area of the spill. In the benthic realm, there was a large loss of diversity of soft-bottom infauna, which were still not recovering a year after the DWH oil spill. Colonial octocorals that are anchored to the hard seafloor and are especially vulnerable to anthropogenic impact, died as a result of being covered with flocculent material containing oil and dispersant. Soft- and hard-bottom effects of the oil spill were found as much as 14 km away from the DWH wellhead site. Deep-sea communities in the Gulf of Mexico are diverse, play critical roles in the food web and carbon cycling, affect productivity, are sensitive to perturbations, and are at risk to contaminant exposure; thus, it is important to understand the effects on these natural resources.

INTRODUCTION

The Gulf of Mexico (GoM) covers approximately 1.6 million km^2 (615,000 square miles), of which almost half is beyond the continental shelf break and generally considered the deep sea. The continental slope, with depths ranging from 180–3,000 m, represents about 20% of the GoM seafloor, and the abyssal plain, which encompasses areas deeper than 3,000 m, comprises another 20% (Gore, 1992). Another way to think about deep GoM ecosystems is to consider the volume occupied by different pelagic habitats. From this perspective, the deep pelagic domain (waters below 200 m depth) is the "typical" pelagic environment in the GoM, representing 90.4% of the GoM's volume (Figure 1). About 30.6% of that volume is mesopelagic (200–1,000 m depth), and 59.8% is bathypelagic (>1,000 m depth). The Deepwater Horizon (DWH) blowout occurred at ~1,500 m depth, which is approximately the center of the continental slope range.

Deep-sea communities are composed of pelagic, demersal, and benthic components that are intricately linked through food webs (Rowe et al., 2008). Assessing damage or change in deep-sea ecosystems is inherently challenging because they are among the most poorly known ecosystems on Earth and are also difficult to visit and sample (Ramirez-Llodra et al., 2010). Good baseline data on deep-sea communities simply do not exist in the vast majority of cases. The deep sea is remote and unseen; most sampling is performed by grabs, trawls, or cameras, which means only tiny fractions of the habitat are ever visualized or sampled. A further complication is that megafauna are patchily distributed, often at low density, in both the pelagial and deep benthos due to the paucity of food sources in the deep sea. The naturally occurring densities of deep-living mobile fauna such as fishes, crabs, and other invertebrates are not only very poorly constrained in general, they exhibit high temporal variability, ranging from the hourly scale (e.g., primary production in the epipelagic), to the diel scale (e.g., vertical migration from the mesopelagic into the epipelagic domain), to the monthly/yearly scale (e.g., organismal horizontal transport in the bathypelagic domain and changes driven by seasonality of primary production and terrestrial input). As a result, detecting changes in local populations or even metapopulations of these mobile groups is problematic and only possible for a very few taxa in very few places for which there are good historic fisheries data.

Outflow from the Atchafalaya and Mississippi Rivers has a large impact on the water quality of nearshore continental shelf environments in the GoM, and also has an important influence on the deep sea. Nutrients are transported far offshore and stimulate phytoplankton blooms that eventually contribute to the flux of organic carbon into deep pelagic waters and deep-sea sediments. This particulate flux supports zooplankton and nekton production and influences benthic meiofauna biomass, productivity, and community structure (Baguley et al., 2008), as well as deep-sea metabolism at all levels, including macrofauna and megafauna (Rowe et al., 2008). Most of the benthos in the deep Gulf of Mexico, like deep-sea benthos elsewhere, depend on the flux of organic materials from surface waters for food. Thus, deep-sea benthos are especially vulnerable to oil spills, like that from the DWH, that lead to the formation of deepwater plumes of oil and gas and the deposition of oil onto the seafloor.

The continental slope of the northern Gulf of Mexico is one of the most geologically complex deepwater settings in the world because of the influence of sediment loading on the underlying mobile Jurassic salt beds (reviewed in Fisher et al., 2007). Large reservoirs of hydrocarbons that overlie the salt beds supply about 95% of all the offshore oil and gas production in US waters. Fractures in the oil-bearing shale resulting from salt bed movement, so-called salt tectonics, provide conduits for hydrocarbons and brines (highly saline water created by the interaction of pore waters with the salt) to migrate upward to the sediment surface, which creates oil and methane seeps and brine pools on the seafloor (McBride et al., 1998). Although unconsolidated sediments, also called soft-bottom muds, cover about 95% of the seafloor in the deep GoM, microbial consortia that oxidize oil and gas at active seeps create conditions that favor carbonate deposition and production of authigenic carbonates. This activity can consolidate sediments and lead to production of massive boulders and slabs. These isolated

hard grounds are widely but patchily distributed among vast areas of unconsolidated sediments throughout much of the deep GoM. The complexity and diversity of these geological features creates a high diversity of benthic habitats, and a highly diverse benthic community compared to coastal benthos.

Over the course of many millennia in the GoM, this combination of tectonic, sedimentary, and geochemical processes has produced numerous areas of hard grounds. Based on acoustic reflectivity in three-dimensional seismic data sets collected in the northern GoM, the Bureau of Ocean Energy Management (BOEM) identified over 23,700 discrete areas likely to host carbonate deposition features in the top 8 m of the seafloor (BOEM, 2016). Although most of these areas no longer release hydrocarbons from the seafloor, and in many cases the acoustically reflective layers are buried by meters of sediment (Fisher et al., 2014a), active seeps are nonetheless widely distributed in the deep GoM (Roberts et al., 2007). In fact, studies using synthetic aperture radar (SAR) imagery identified 914 areas in the GoM where natural oil seepage produces a signature visible on the sea surface (MacDonald et al., 2015).

A variety of benthic fauna in the GoM uses the energy and carbon from natural seeps through chemoautotrophic and/or methanotrophic primary production (Childress et al., 1986), which can create localized high-biomass communities (Cordes et al., 2009). This benthic primary production is also an important subsidy to the organic matter produced in surface waters that sediment-dwelling communities rely upon in some areas. However, the effects of seeps in the deep GoM are highly localized. For example, although corals are often found in areas near active seeps, with the exception of one species, there is no isotopic signal of seep primary production in the corals or the fauna closely associated with them (Becker et al., 2009). Similarly, in 20 m water depth off Coal
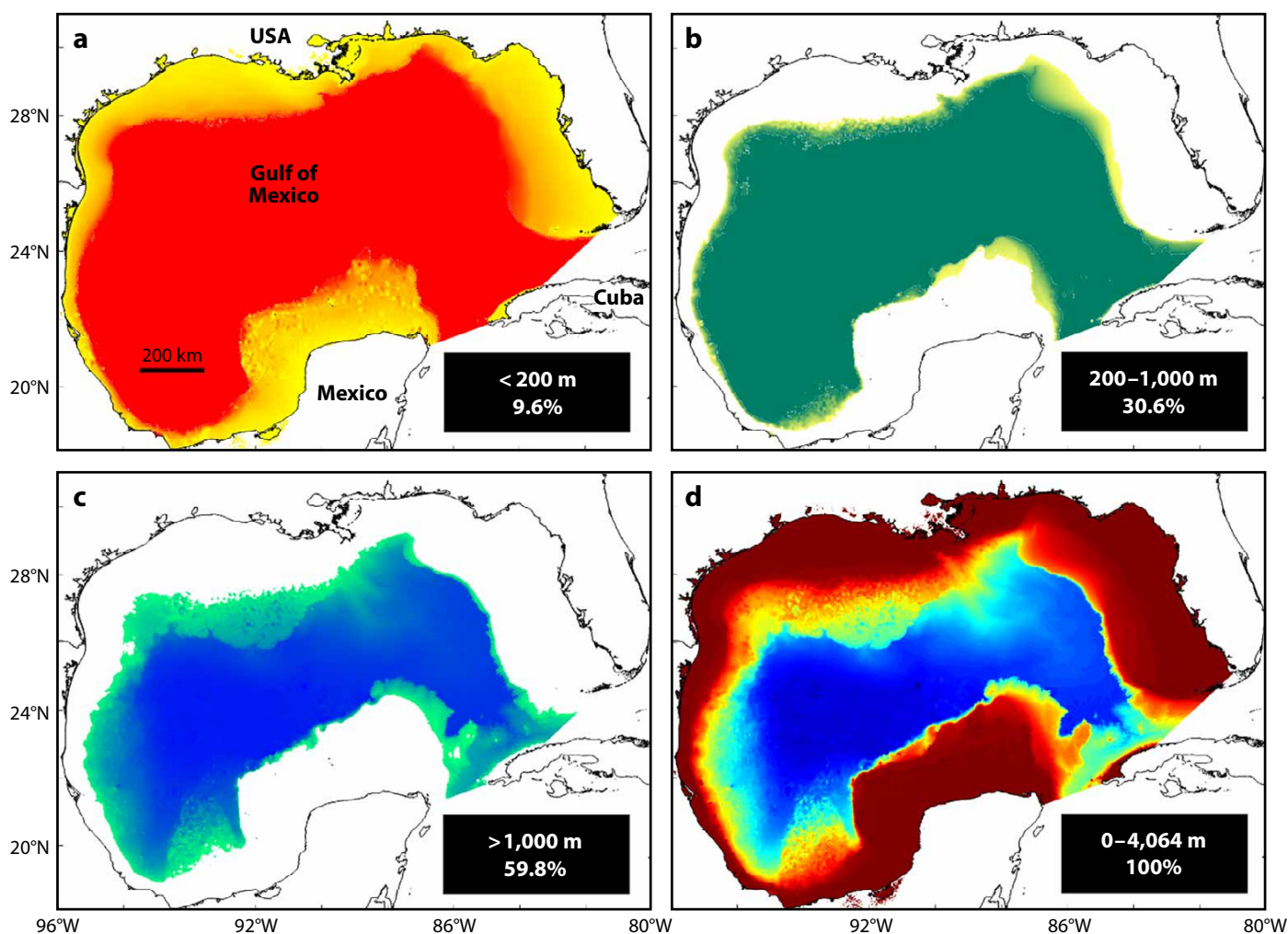

FIGURE 1. Percent volumes of water within various depth strata within the Gulf of Mexico: (a) 0–200 m, (b) 200-1,000 m, (c) >1,000 m, (d) all depths. From the perspective of the volume occupied by different pelagic habitats, the deep pelagic domain (waters below 200 m depth) is the "typical" pelagic environment in the GoM, representing 90.4% of the its volume. About 30.6% of that volume is mesopelagic (200–1,000 m depth), and 59.8% is bathypelagic (>1,000 m depth). The Deepwater Horizon blowout occurred at ~1,500 m depth, which is approximately the center of the continental slope range. *Figure produced by Matthew Johnston for DEEPEND Consortium (www.deependconsortium.org) using 30 arc second bathymetry data from http://gcoos.tamu.edu/products/topography/SRTM30PLUS.html*

Oil Point (Santa Barbara, California), oil seeps affect metabolism (Montagna et al., 1986) and community structure of benthos (Montagna et al., 1987) only within about 10 m of the seep.

THE PELAGIC REALM

From a spatiotemporal perspective, the deep pelagic realm is among the most complex ecosystems in the GoM. In the vertical dimension, the deep GoM region varies from the brightly lit, warm epipelagial, to the dimly lit, thermally variable mesopelagial, to the lightless, ever-cold bathypelagial. As noted above, ecological processes within each of these depth domains also exhibit high temporal variability on scales ranging from hours to years. When the near-absence of baseline information on the deep-living communities is coupled with this spatiotemporal complexity, it is easy to grasp the inherent difficulty of assessing the impact of the DWH oil spill on GoM deep pelagic ecosystems. Below, we review what is known about key faunal constituents of the pelagic GoM, both before and after the DWH oil spill, with the proviso that much of what we have learned is post-DWH oil spill, and many of the syntheses are still in progress.

Epipelagic Domain

The epipelagic GoM represents two faunal communities, depending on the time of day. During the day, the epipelagial contains the primary producers (phytoplankton), the majority of the secondary producers, a diverse array of larval and holoepipelagic fishes (Sutton, 2013), and specialized higher vertebrates (e.g., marine mammals; Jefferson and Shiro, 1997). At night, the epipelagic contains these components plus a massive influx of animals from meso- or bathypelagic depths, the "nyctoepipelagic" diel vertical migratory fauna that either feed on zooplankton or on organisms feeding on zooplankton (Sutton et al., 1998).

Graham et al. (2010) demonstrated that below the water's surface, oil carbon was incorporated into the coastal plankton food web. Given the preponderance of microbial mediators in the pelagic environment, it would be expected that oil carbon would similarly be incorporated into the epipelagic food web at some level via microbial-mesozooplankton trophic linkages. Hu et al. (2011) suggested that this incorporation of petrochemicals may have reduced mesozooplankton grazing pressure, resulting in the anomalously high phytoplankton biomass detected after the DWH spill, though they cited the lack of sufficient data to support or reject this hypothesis. Dispersants and oil resulted in an increase in biomass of heterotrophic prokaryotes and a decrease in ciliates, indicating a reduction in grazing pressure and a decrease in transfer of carbon to higher trophic levels (Ortmann et al., 2012). A simulation analysis of pelagic plankton dynamics after the DWH oil spill (Walsh et al., 2015) highlighted the difficulty in specifically ascribing this spill as a driver of plankton production variability in an ecosystem that is already unbalanced as a result of a wide range of forcing agents (e.g., freshwater nutrient loading, other pollution, overfishing, and climatic effects). *Sargassum*, a brown alga, provides a floating habitat for a diverse array of sea creatures. Mats that came into contact with surface oil and dispersants not only stressed animals that depended on this ocean habitat by exposing them to toxins but also caused *Sargassum* to sink, creating a low dissolved oxygen environment on the seafloor as the mats decomposed (Powers et al., 2013).

The epipelagic GoM hosts a diverse fish fauna, many of which are economically important. Both before and after the DWH oil spill, Rooker et al. (2013) examined larval abundances of four such species (blue marlin, *Makaira nigricans*; Atlantic sailfish, *Istiophorus albicans*; blackfin tuna, *Thunnus atlanticus*; and common dolphinfish, *Coryphaena hippurus*). They found no significant reductions in larval abundance after the DWH spill, citing high subannual (monthly) variability within years as an obfuscatory

factor. Tracking experiments by these authors revealed that the spatial extent of the DWH oil spill overlapped with adult blue marlin habitat, and that occurrence of marlin in areas impacted by the DWH was lower after the spill, though significance was not determined. Oil exposure tests performed on pelagic fish species (e.g. tunas and jacks) in Mississippi Canyon lease block 252 (MC252) revealed developmental crude oil cardiotoxicity (Incardona et al., 2014), suggesting that there was likely a loss of early recruits of many epipelagic predators that spawn in the open GoM. The Gulf of Mexico Research Initiative (GoMRI) Relationships of Effects of Cardiac Outcomes in fish for Validation of Ecological Risk (RECOVER) Consortium (http://www.recover.rsmas.miami.edu) is currently using the common dolphinfish (mahi-mahi) as a model organism to examine the effect of oil on economically important fishes. Incorporation of oil into the food web led to closure of fisheries for one year around the wellhead and longer in some parts of coastal Louisiana (Ylitalo et al., 2012).

Twenty-nine species of cetaceans have been reported in the GoM, most of which occupy the oceanic domain for all or part of their lives (Wynne and Schwartz, 1999). Though abundances of these taxa were monitored prior to the DWH spill, the low precision of these abundance estimates would allow only a catastrophic die-off to be detectable through population censuses (Taylor et al., 2007). Further, mortalities due to the DWH oil spill were difficult to assess. For example, Williams et al. (2011) used population dynamics data to estimate that in general, only 2% of cetacean carcasses are recovered from mortalities. Their estimate suggests the true death toll of cetaceans could have been much (e.g., 50 times) higher than the 140 mortalities attributed to oil one year after the spill (US Fish & Wildlife Service, 2011), though these authors caution that coordinated interdisciplinary research is required to estimate mortalities from carcass-detection

rate multipliers. The data required to permit comparison of pre-spill and post-spill mortality rates using the multiplier technique are not currently available for primarily oceanic cetaceans, as the bulk of recovered carcasses were of bottlenose dolphins (Williams et al., 2011).

Studies of sperm whale (*Physeter microcephalus*) distribution in the northern GoM suggest that the Mississippi Canyon area has been an important foraging habitat (Davis et al., 1998). Their primary prey includes deep pelagic cephalopods and various fishes (Judkins et al., 2015) gathered during long (>2 h), deep (>1,600 m) dives. Ackleh et al. (2012) reviewed pre- and post-DWH oil spill acoustic recordings around the area of the spill and found that cetacean acoustic activity nearer the spill site decreased by a factor of two post-spill, while activity farther from the site increased, suggesting that sperm whales may have relocated farther away from the spill. This hypothesis is being investigated by members of the

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GoMRI Littoral Acoustic Demonstration Center-Gulf Ecological Monitoring and Modeling (LADC-GEMM) Consortium (http://www.ladcgemm.org), who are establishing a long-term monitoring program to more fully elucidate the impact of the spill on regional marine mammal populations in the GoM.

Mesopelagic Domain

Most of the quantitative information on the mesopelagic fauna of the GoM prior to the DWH oil spill is derived from Thomas Hopkins' 30-year (1970–2000) program in the eastern Gulf, at a site referred to as "Standard Station" (27°N, 86°W). This program focused primarily on the faunal composition, vertical distribution, and trophic interactions of the zooplankton and micronekton (smaller fishes, crustaceans and cephalopods) from 0–1,000 m depth (see references in Hopkins et al., 1996). The published works from this program characterize assemblages of high mesopelagic species richness (e.g., Sutton and Hopkins, 1996) at multiple trophic levels that exhibit a high degree of niche partitioning in time, space, and food resources. Whole water-column carbon flux modeling by Rowe (2013) suggested that most of the particulate organic carbon production in the oceanic GoM is consumed by zooplankton and mesopelagic fishes (see title page photo) down

to the maximum depth of plankton between 100 m and 1,000 m, and the rest is largely consumed by the bathypelagic fauna. The majority of mesopelagic taxa perform vertical migrations from below 600 m during daytime to above 200 m at night (Hopkins et al., 1996), which greatly increases the probability of these

fauna encountering subsurface oil plumes at the bottom of their range and oil-contaminated plankton in the shallower waters. Regarding higher trophic levels (4° and higher), mesopelagic fishes (especially lanternfishes, Myctophidae) dominate the remains of small fishes found in cetacean stomachs (Fitch and Brownell, 1968) and are important prey for larger pelagic species such as tunas and billfishes (Allain, 2005).

Standard Station is located ~304 km southeast of the Macondo wellhead site, but drifter studies from the GoMRI Consortium for Advanced Research on Transport of Hydrocarbon in the Environment (CARTHE: http://www.carthe.org) indicate that this region likely received some amount of subsurface hydrocarbons from the DWH oil spill, though there was considerable variability in the estimated quantities per location, depending on the source of the analysis (see Figure 1 in Mariano et al., 2011). As such, data from this program represent a potential baseline for comparison with data acquired the year after the DWH spill (D'Elia et al., 2016) and data from sampling currently in progress (2015–2017) by the GoMRI Deep-Pelagic Nekton Dynamics (DEEPEND) Consortium (http://www.deependconsortium.org). Other sources of quantitative data for ongoing comparative community analyses, collected on smaller spatiotemporal scales in the northern GoM, include the discrete-depth surveys of Wormuth et al. (2000) and Ross et al. (2010).

While ongoing efforts are attempting to determine the community-level effects of the DWH oil spill on the mesopelagic fauna via time-series analysis, Quintana-Rizzo et al. (2015) demonstrated the incorporation of carbon from the spill into the mesopelagic food web. These authors concluded that because most of the mesopelagic community is planktivorous (or feeds directly on zooplanktivores) in the upper 200 m at night (Hopkins and Sutton, 1998, and references therein), the shift detected in their isotopic signatures likely resulted from consumption of

prey rich in depleted carbon from the dispersed oil. This incorporation of oil in the food web indicates that, at the least, sublethal effects of the DWH oil spill were present in the deep pelagic domain.

Bathypelagic Domain

The presence of large plumes of dissolved hydrocarbons between 1,000 m and 1,300 m depth as a result of the DWH oil spill has been widely reported (e.g., Diercks et al., 2010). Microbial communities that developed within these plumes differed from those found in non-plume waters (e.g., Valentine et al., 2010). The effects of the DWH oil spill on pelagic metazoans, however, are largely unknown due to a lack of quantitative baseline data. Quantitative, discrete-depth data on the bathypelagic metazoan fauna of the GoM prior to the DWH oil spill is limited to a single published study by Burghart et al. (2010), conducted in the latter years (1990s) of Hopkins' program at Standard Station. This study found that the micronekton assemblage was dominated by fishes, primarily bristlemouth fishes (Stomiiformes, Gonostomatidae, *Cyclothone* spp.), but macrocrustaceans (lophogastrids and decapod shrimps) were also relatively common. Trophic analysis of the dominant taxa revealed that detritus and cnidarian material were prevalent diet components. This finding suggests a possible transmission vector between MOSSFA (marine oil snow sedimentation and flocculent accumulation; e.g., Passow et al., 2012) and the bathypelagial fauna. The Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG; https://ecogig.org) and Aggregation and Degradation of Dispersants and Oil by Microbial Exopolymers (ADDOMex; www.tamug.edu/addomex) consortia are continuing to conduct research into the effects of oil and dispersants on the formation and fate of marine snow, associated microbes, and benthic communities.

Given the lack of pre-DWH oil spill bathypelagic faunal data, and the prominence of the spill as a bathypelagic phenomenon, the National Oceanic and Atmospheric Administration (NOAA) Office of Response and Restoration facilitated creation of the Offshore Nekton Sampling and Analysis Program (ONSAP; for ONSAP work plans, see http://www.gulfspillrestoration.noaa.gov/oil-spill/gulf-spill-data). At the time of this writing, all ONSAP sample processing has been completed and publication of results and further analyses are underway. Initial results of this program confirm the notion that the bathypelagic domain is the GoM's most undersampled ecosystem, despite being the largest; of the 460 fish species collected during the Natural Resource Damage Assessment 10 m^2 MOCNESS spring 2011 survey series, 50 were previously unknown for the GoM, and the majority of these were bathypelagic (Sutton and Hopkins, 1996; Yang and Huang, 1986; Flynn and Kloser, 2012), including undescribed species (Pietsch and Sutton, 2015). The species composition results also confirm the designation of the GoM as one of the most diverse deep pelagic ecoregions of the world ocean, with species richness greater than, or on par with, the Tasman Sea, South China Sea, mid-Indian Ocean, and the Guinea Basin/East Equatorial Atlantic (recent work of author Sutton and colleagues). As with the mesopelagic zone, comparison of 2010–2011 bathypelagic data with ongoing sampling and analysis will be a focus of the DEEPEND Consortium.

Benthopelagic Domain

As with many of the deep-pelagic taxa, the status of the benthopelagic fish fauna of the deep GoM (e.g., sharks, skates, rattails, eels) is largely unknown due to data deficiency (Kyne and Simpfendorfer, 2010), though post-spill research has provided new insights into the ecology of some taxa. Churchill et al. (2015) examined the trophic ecology of common deepwater sharks in the northern and eastern GoM and found no difference in feeding of these taxa before and after the spill. Their results also highlighted the importance of trophic coupling between the benthopelagic fauna and the overlying deep pelagic fauna (particularly myctophids as prey). Ongoing research at Florida State University, University of North Florida, Mote Marine Laboratory, and Florida International University is assessing the oil exposure of deepwater fishes using polycyclic aromatic hydrocarbon (PAH, a persistent organic pollutant) "biomarkers," which will increase our understanding of the effects of the DWH oil spill on the deep demersal fauna.

THE BENTHOS

An amazing fact about the DWH oil spill is that a lot of the oil never left the deep sea, and a significant proportion of what reached the surface subsequently returned to the deep sea. The deep-sea plume resulting from the oil released into the deep ocean covered about 930 km^2 (360 square miles). A lot of spill residue wound up on the bottom of the ocean as a result of both a large marine oil snow sedimentation event termed the "dirty blizzard" and by direct contact of the oil-laden deep plume with continental slope surface sediments forming a "bathtub ring" of oil (Valentine et al., 2014). These contaminants pose risks to benthic fauna, particularly those living within or in close association with bottom substrates and unable to avoid exposure due to their relatively sedentary existence.

The diverse deep-sea benthic fauna is composed of bacteria, protists (especially foraminifera), meiofauna, macrofauna, and megafauna. For all benthic organisms, there are strong relationships between abundance, biomass, and diversity with latitude and longitude. In the GoM, the latitudinal gradient is generally driven by depth relationships, and the longitudinal gradient is driven by the influence of the Mississippi River, which is in the center of the northern GoM. Bacterial biomass and respiration in sediments increase with increases in organic material flux in the central part of the GoM near the Mississippi River. There is also higher biomass and productivity in meiofauna in the central than in the eastern or western GoM. Bacterial biomass in

deep-sea sediments decreases with depth from 300 m to 3,900 m because although cell density stays the same, cell sizes are smaller (Deming and Carpenter, 2008). Meiofauna abundance decreases linearly with depth from 300 m to 3,900 m. While richness (i.e., species number) of harpacticoid copepods decreases with depth (and decreasing density), diversity indices that are based on phylogenetic or taxonomic distinctness increase with depth. The trends for Harpacticoida are also true for benthic foraminifera, nematodes, and benthic macrofaunal isopods. Diversity indices peak at around 1,500 m depth, which means the DWH blowout occurred in the most ecologically diverse region of the deep Gulf of Mexico.

Soft-Bottom Community Response

The release of oil and gas from the DWH stimulated bacterial respiration and caused lower dissolved oxygen concentrations in the deep GoM (Du and Kessler, 2012). Lower dissolved oxygen concentration, coupled with rapidly sinking marine oil snow (Passow et al., 2012), deposition of oil onto the seafloor (Valentine et al., 2014), and the release of heavy metals associated with drilling and attempts to cap the well, made areas of the deep GoM seafloor resemble a toxic waste dump. The addition of dispersants likely increased the water-soluble fraction of oil, further stimulating microbial respiration. The increase in hydrocarbon concentrations on the seafloor led to increased oxygen consumption (Main et al., 2015), and the decrease in oxygen altered microbial communities and caused an increase in denitrification processes and the net accumulation of dinitrogen (Scott et al. 2014). Thus, the oil spill likely changed the nature of microbial communities in the deep sea. There was an 80%–93% decline in benthic foraminifera following the DWH event related to persistent reducing conditions and increased PAH concentrations (Schwing et al., 2015).

The most severe relative reduction of benthic macro- and meiofaunal diversity occurred within 3 km of the wellhead

(−54% and −38%, respectively), over an area of about 24 km^2 (about nine square miles; Figure 2; Montagna et al., 2013). Moderate impact areas, where diversity decreased for macrofauna (−5%) and meiofauna (−19%), were observed up to 17 km toward the southwest and 8.5 km toward the northeast of the wellhead, over a 148 km^2 area (about 57 square miles, which is larger than the island of Manhattan). Benthic effects were correlated to total petroleum hydrocarbon, PAH and barium concentrations, and distance to the wellhead, but not distance to natural hydrocarbon seeps in the area. Thus, benthic effects are attributed to the oil spill and not to natural hydrocarbon seepage.

The macrofauna loss was primarily in surface sediments (Washburn et al., 2016). There was a larger proportion of animals in the top 5 cm of sediment vs. deeper (5–10 cm) at stations further from the wellhead, and communities were significantly different among impact areas in the surface sediments but not the deeper sediments. Dorvilleidae, a polychaete family often associated with hydrocarbons (Hyland et al., 1994; Washburn et al., 2016), was responsible for the largest amount of dissimilarity between stations close to the wellhead and further away. Several other taxa were classified as sensitive or tolerant to the deep-sea blowout by comparing their distributions among impact and nonimpact zones. Crustacean taxa appeared to be generally sensitive to the deep-sea blowout, but polychaete taxa varied in their sensitivity. Community structure among different impact zones was highly correlated with several physical and chemical parameters, including barium and biphenyl, which are often associated with drilling activities.

A subset of stations sampled in 2010 was resampled in May–June 2011 and May–June 2014 to determine if the adverse effects were persisting (Montagna et al., 2016a). Experimental design was to compare 20 stations from the combined moderate and severe impact zone

to 12 stations in the reference zone that were sampled in both years. There were no statistically significant differences in contaminant concentrations within the impact zones from 2010 to 2011, indicating contaminants persisted after one year. While there were some signs of recovery in 2011 (particularly for the meiofauna), there was evidence of persistent, statistically significant impacts to both the macrofauna and meiofauna. Macrofaunal taxa richness and diversity in 2011 were still 22.8% and 35.9% less, respectively, in the entire impact zone than in the surrounding area, and meiofaunal richness was 28.5% less in the entire impact zone compared to the surrounding area. The persistence of significant biodiversity losses nearly one year after the wellhead was capped indicates that full recovery had not yet occurred in 2011. Macrofauna and meiofauna diversity had not recovered after four years and community structure differences from background still persist (Montagna et al., 2016b).

Surveys performed with remotely operated vehicles showed that deep-sea megafauna also had lower diversity and abundances in the region of the oil spill relative to regions further away (Valentine and Benfield, 2013). Demersal fishes were also affected by the oil spill. For example, the burrow-forming golden tilefish were persistent and had among the highest concentrations of naphthalene metabolite levels measured in fishes globally (Snyder et al., 2015).

Deep-Living Coral Communities

Although coral communities associated with small and patchy hard grounds in the deep GoM are generally as poorly known as the communities discussed above, projects funded by the BOEM over the last decade have identified and characterized many of these communities in the deep sea. Deep-sea colonial corals, in particular octocorals, have proven to be an excellent group for detecting impact to hard ground ecosystems. These colonial animals normally live from hundreds to thousands of years (Prouty et al., 2011,

2014). Their soft tissues are largely outside of their skeletons and are relatively permeable because gas exchange occurs across their body surfaces, and thus they are constantly "sampling" the epibenthic water. The larger colonial corals are easily visible in their natural habitats, and acute visible damage to a colony is also relatively easy to detect and quantify. Furthermore, when damaged or even killed, their skeletons remain in place for many years, providing records of past events (Hsing et al., 2013). Thus, these animals are excellent sentinels for anthropogenic impacts in the deep sea (Fisher et al., 2014a). Furthermore, because they are interacting with the epibenthic water, corals may detect nondepositional events associated with passing water parcels that do not leave detectable signatures in seafloor sediments.

As part of an ongoing BOEM study of deep coral ecosystems, in November 2010, a team of scientists visited 15 known sites in the GoM that support deep coral communities at depths between 250 m and 2,500 m. Because of the timing of this previously scheduled cruise, the scientists used this opportunity to look carefully for any visible evidence that the DWH oil spill had an impact on these coral communities. No evidence of damage to any of the previously known sites was detected, including a rich coral community less than 38 km to the north of the Macondo well at 1,360 m depth (Brooks et al., 2016). However, during the last dive of this expedition, explorations in an area 13 km to the southwest of the Macondo well discovered a coral community with obvious visible evidence of recent deleterious impact to the corals (White et al., 2012a,b). Samples of flocculent material that were removed from these corals in December of 2010 were found to contain oil that had fingerprint characteristics of Macondo oil (White et al., 2012a) as well as dioctyl sodium sulfosuccinate (DOSS), a long lasting component of the Corexit dispersant used during the spill (White et al., 2014). This coral community has now been visited eight times, and during every visit, as many corals as possible have been photographed in order to follow the progression of results from the original impact to this community. Between 2010 and 2012, the average level of visible impact to the corals decreased, because some parts of the colonies that were covered with floc in 2010 recovered after the flocculent material fell off of them (Hsing et al., 2013). However, in many areas of the impacted colonies, the tissues had died, and in some cases the skeletons were secondarily colonized by hydrozoans. Hsing et al. (2013) found that both recovery and level of secondary hydroid colonization by 2012 were correlated with the degree of initial impact visualized in 2010. These studies have continued with support from
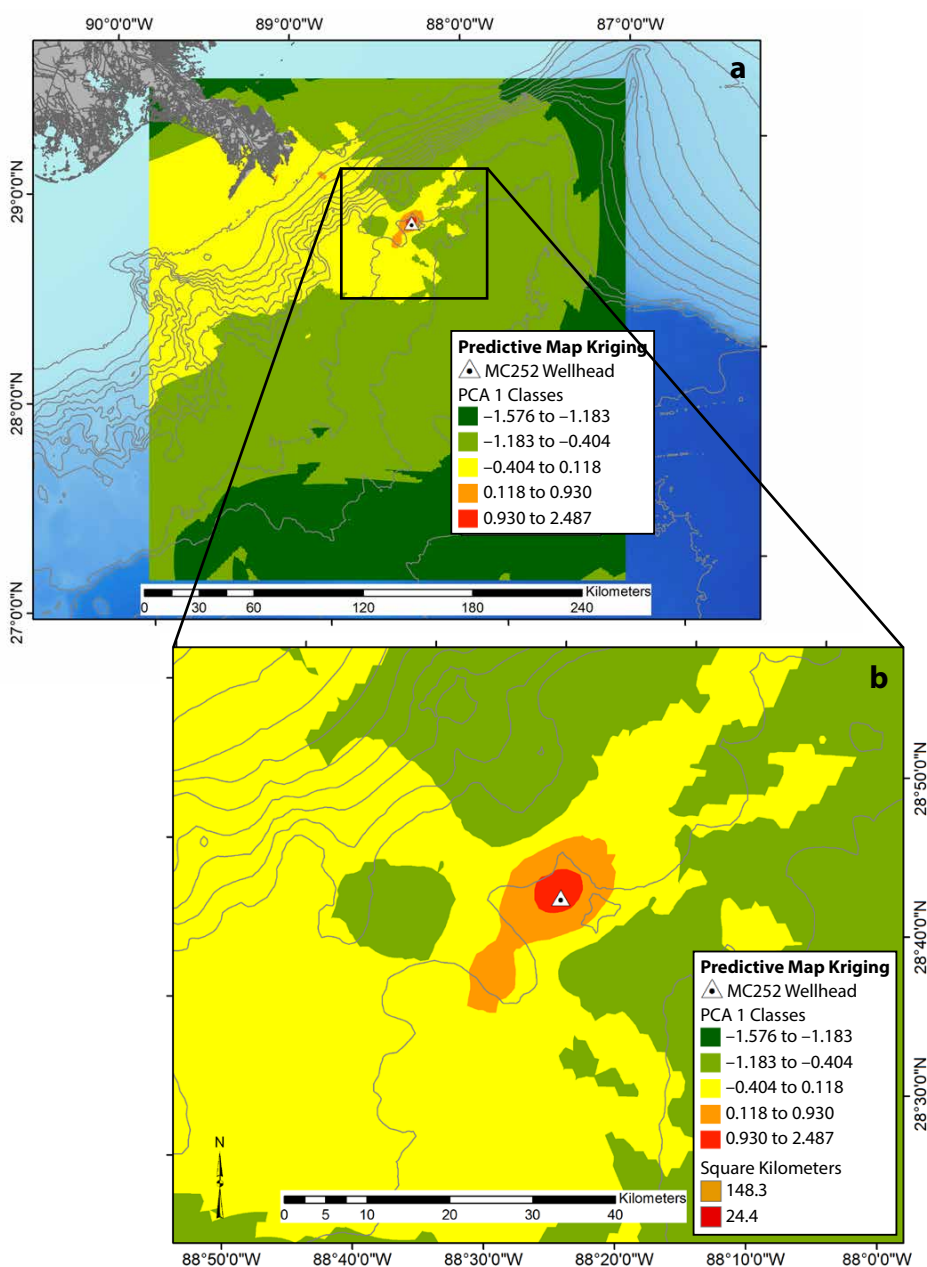

FIGURE 2. (a) Interpolated area of deep-sea impact based on multivariate analysis of station scores (PCA 1). The interpolated area shown covers 70,166 km[2] of which 167 km[2] (orange) are considered moderately impacted by the Deepwater Horizon oil spill, and 24 km[2] (red) are considered severely impacted. (b) Zoomed-in view of the interpolated area of deep-sea impact. The shape of the moderate impact area is asymmetrical, extending further to the southwest (about 17 km from the wellhead) than to the northeast (about 8.5 km from the wellhead). The diameter of the severely impacted zone (in red) is about 4 km. *Source: Montagna et al. (2013)*

GoMRI to the ECOGIG I and II consortia and are not only providing data on the ultimate fate of the impacted corals but also have documented the beneficial effects of colonization by commensal ophiuroids (brittle stars), which both provide some protection from impact and facilitate recovery from hydroid colonization (Girard et al., 2016). Analyses of the rich data set of over 350 individual colonies imaged each year are also providing new insights into longer-term effects of hydroid colonization on octocorals, the patterns and tempo of branch loss following branch death in deep-sea octocorals, and growth rates and growth patterns of both impacted and non-impacted deep-sea corals (Figures 3 and 4).

These time-series studies also allowed researchers to document impacts to other sites found years after the DWH spill. The distinctive impact patterns and docu-

impacted than the corals in the community discovered in 2010. This discovery clearly refuted the suggestion put forward by Boehm and Carragher (2012) that the impact discovered at the single site in 2010 was coincidental and not due to the DWH oil spill. Another site, with corals showing the characteristic signs of impact from the spill was discovered in 2011, 22 km to the east of the Macondo wellhead, in much deeper water (1,850 m depth) than was likely to directly come in contact with the deepwater oil and gas plume that formed during the spill (Reddy et al., 2011; Fisher et al., 2014b). Continued observations collected under the GoMRI ECOGIG I and II programs have revealed numerous additional impacted coral colonies at both of these sites that further implicate the spill as the cause of the damage to these communities. Investigation of other potential

work provides insights into the potential impact footprint on coral communities in the deep sea. These researchers used generally similar techniques to detect and quantify damage, and like the studies on the deeper living corals, they benefited from the fact that the skeletons recorded impacts from earlier events. Imagery from the mesophotic sites prior to the spill also allowed these researchers to use a BACI (before-after-control-impact) approach in their analysis, a powerful method that is not possible to use on the newly discovered communities in deeper water closer to the Macondo well. However, these shallower coral communities also apparently are subject to a much higher level of "background" impact, which could be due to a variety of natural or anthropogenic stressors associated with life on the shallower shelf, but not the spill itself. As a result, the authors are cautious in their interpretation of changes in impact levels to these ecosystems between 1999 or 2003, and 2011. Nonetheless, they conclude that the most parsimonious explanation for their findings is that the corals were impacted by oil originating from surface slicks over these sites as a result of dispersant application, surface burning of the oil, or enhanced delivery of the surface oil to the seafloor during Tropical Storm Bonny in July 2010.

As for the case of the mesophotic reefs, a deepwater plume of oil/gas/dispersant is not the most likely cause of the negative impact to the MC344 coral community discovered 22 km to the east of Macondo in 1,850–1,950 m water depth (Fisher et al., 2014b). Similar to the damaged mesophotic reefs, the MC344 coral community was in an area beneath surface oil slicks for an extended period of time and where dispersant was applied to the surface slicks numerous times. The patchy nature of the impact to the community and individual corals at this site and at the mesophotic reef sites, and even at the deepwater sites closer to the Macondo well, is consistent with impact from an agent that was patchily distributed in the bottom waters, perhaps toxic marine

> " The persistence of significant biodiversity losses nearly one year after the wellhead was capped indicates that full recovery had not yet occurred in 2011. Macrofauna and meiofauna diversity had not recovered after four years and community structure differences from background still persist. "

mented changes over time to the affected corals can be used to link impacts on newly discovered communities from the same event. Using this approach, two additional coral communities that were affected by the DWH oil spill were discovered (Fisher et al., 2014b). One of the coral communities found in 2011 was 6 km to the south of the Macondo wellhead and 13 km from the first site discovered in 2010 at 1,560 m depth. Corals at this site were in general more heavily

coral sites in the region is ongoing to better define the footprint of acute impact to benthic megafauna.

Other researchers working in much shallower waters (between 68 m and 88 m depth) have also documented extensive damage to coral communities on mesophotic reefs after the spill (Etnoyer et al., 2015; Silva et al., 2015). Although these are not deep-sea communities, they are sufficiently removed from contact with surface waters such that this
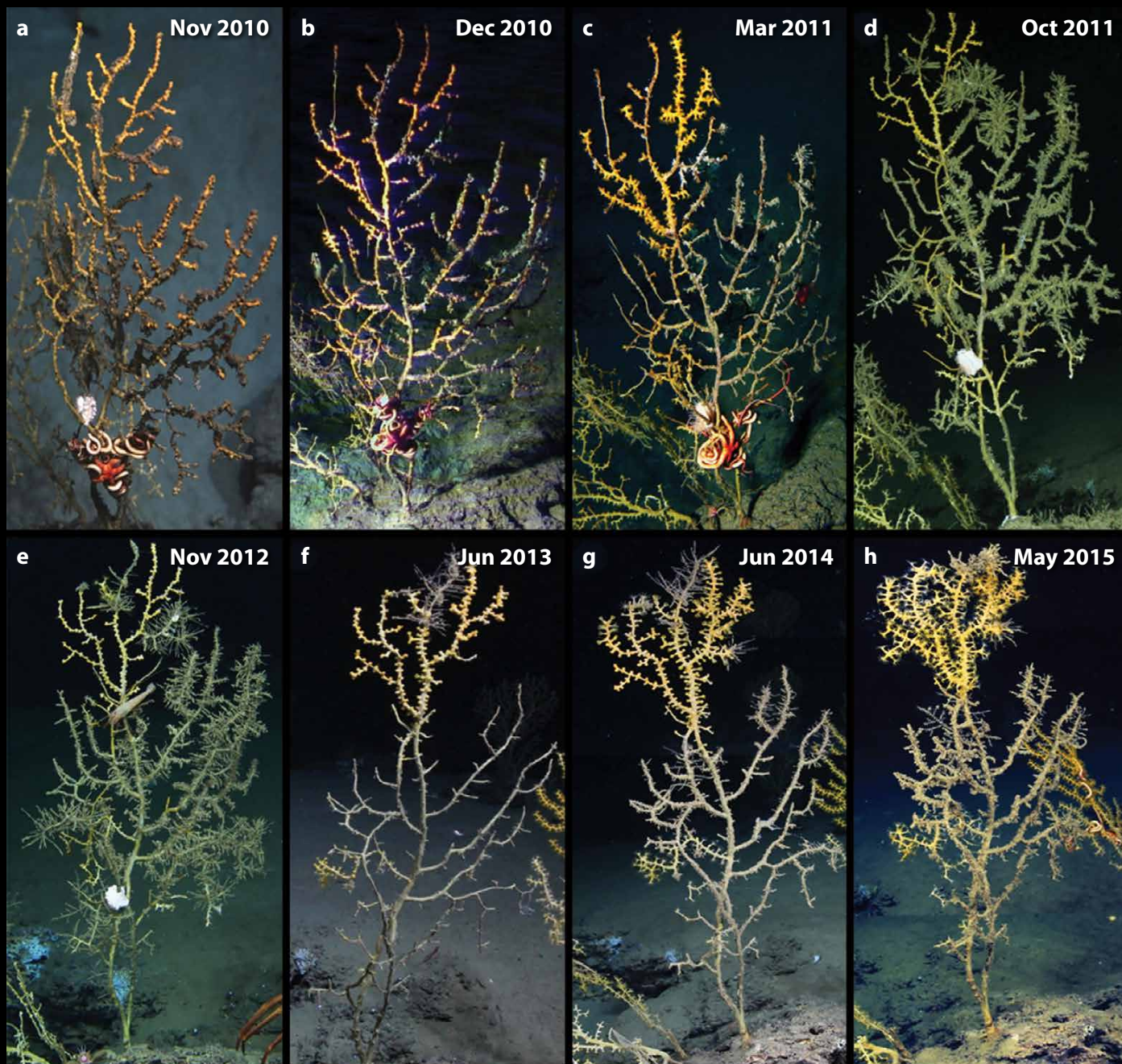
FIGURE 3. Photos over time of *Paramuricea biscaya* colony D3 from the first impacted community discovered. The trend seen on this individual coral is typical of the more heavily impacted octocorals at two other coral sites nearest the Macondo well. Note that this coral is partially covered by flocculent material in 2010, which resulted in mortality of many branches by March of 2011. By October 2011, this coral was colonized by hydroids, and the hydroid populations subsequently waxed and waned over time. The commensal ophiuroid present in 2010 disappeared between March and October 2011, and the commensal anemone was lost between November 2012 and June of 2013. Loss of terminal branches began in 2011, with larger branches disappearing after November 2012 and continuing through 2015. Note also the limited recovery of coral tissue in some areas adjacent to living coral polyps. *Figure courtesy of F. Girard, Penn State*

snow. This mechanism of transfer of toxic material to the deep sea could greatly increase the footprint of impact to some types of communities in the deep sea.

WHY CARE ABOUT THE DEEP GULF OF MEXICO?

Deep-sea fauna serve vital functional roles in deep-sea ecosystems, including biomass production, sediment bioturbation and stabilization, organic matter decomposition, nutrient regeneration, and secondary production (Danovaro et al., 2008). The primary challenges in identifying and articulating the benefits of ecosystem services emanating from the deep sea are the many knowledge gaps around the functioning of deep-sea ecosystems, including those of the GoM, and the prevalence of intermediate services relative to final services (Armstrong et al., 2012). Intermediate services include the biologically mediated habitat, nutrient cycling, resilience and resistance, and water circulation and exchange (Jobstvogt et al., 2014), whereas final services include carbon storage and sequestration, food provision, genetic resources, and waste absorption and detoxification (Ramirez-Lodra et al., 2011; Jobstvogt
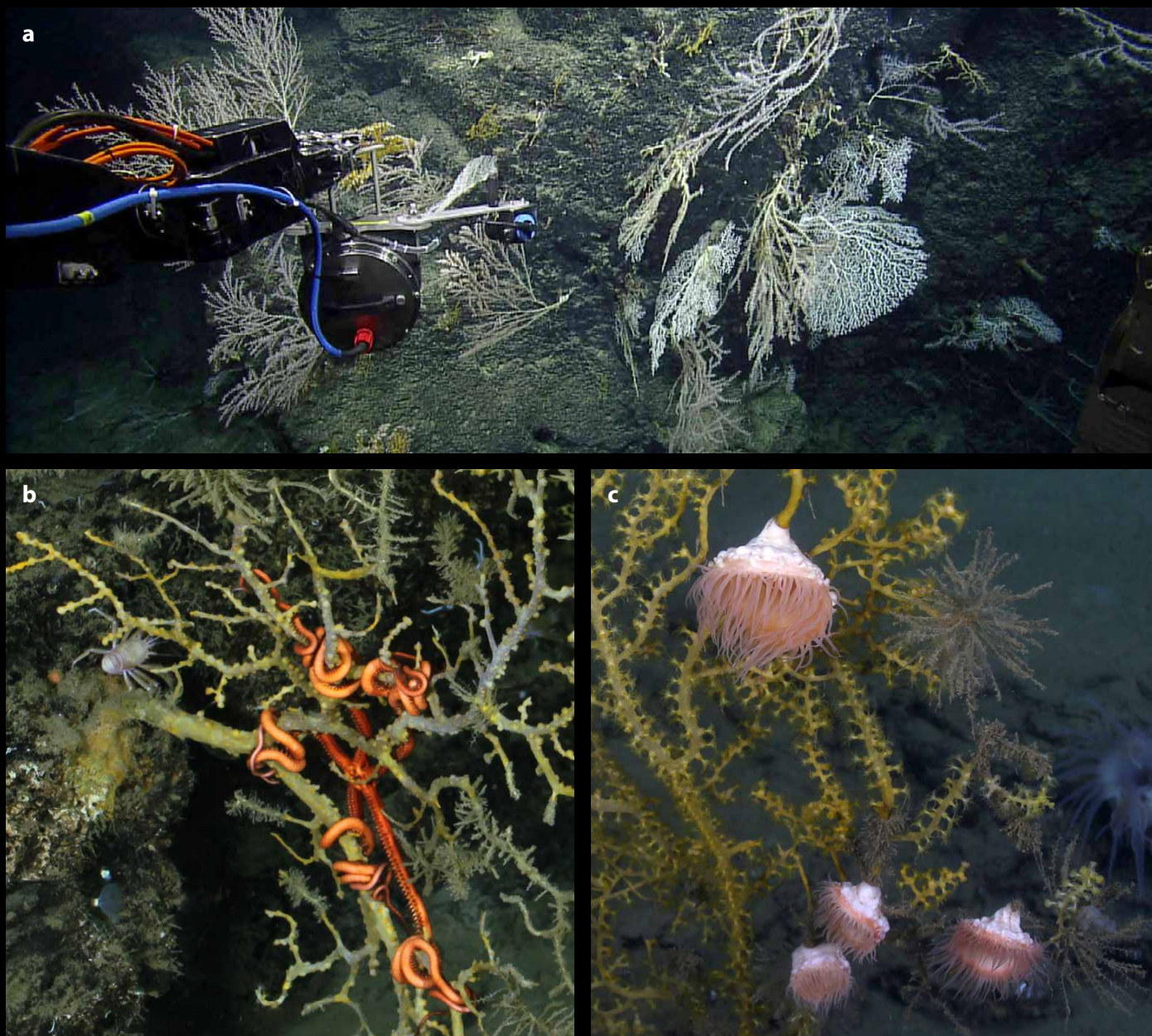
FIGURE 4. (a) Frame grab from a high-definition camera on the remotely operated vehicle *Hercules*, showing an Aquapix digital still camera taking photos to assess coral damage. *Photo courtesy of the Ocean Exploration Trust* (b) Example of the commensal ophiuroid *Asteroschema clavigerum* (brittle star) on a coral impacted by the Deepwater Horizon oil spill. (c) *Paramuricea biscaya* coral with associated biota (anemones). Note the brown hairy-looking material on the right branch of the coral are hydroids that settled on dead parts of the corals, demonstrating the patchy pattern of damage. *Photos (b) and (c) courtesy of C. Fisher and the Ocean Exploration Trust*

et al., 2014; Thurber et al., 2014). In the deep GoM, a primary biological mediation is the provision of foraging grounds for commercially valuable epipelagic fishes (e.g., bluefin tuna, *Thunnus thynnus*) and aesthetically/spiritually valued cetaceans. In many ocean regions, including the GoM, the bathypelagic and benthos represent important reservoirs of marine biodiversity and, as noted above, the spill occurred in the region of highest benthic species diversity reported for the GoM. The loss of biodiversity is correlated to an exponential decline in deep-sea ecosystem functioning (e.g., nutrient and carbon cycling; Danovaro, 2008) and reduces the resilience of deep-sea ecosystems and their ability to respond to disturbance (Levin and Dayton, 2009; Leduc et al., 2012). The deep sea absorbs ~25% of anthropogenic carbon emissions (Canadell et al., 2007; Sabine and Feely, 2007), a critical service that influences climate. The GoM is a prime example of waste detoxification services provided by the deep sea; microbial communities degraded hydrocarbons released by the DWH oil spill (Valentine et al., 2010; Lu et al., 2012). The deep sea also provides cultural (nonmaterial) services for humans in the form of intrigue and excitement of discovery (e.g., Bell et al., 2016), which often drives technological advancement. Educational, technological, and scientific advancement inspired by this excitement has driven substantial economic investment in the form of physical (ships, sensors, gear) and academic infrastructure. In short, deep-sea ecosystem services are vital to human well-being. As we move forward, it will be important to consider ecosystem services frameworks that can be used to quantify the monetary value of the deep-sea in the course of its study (Thurber et al., 2014).

Because deep-sea communities in the GoM are diverse, are a critical part of the food web base, play a key role in carbon cycling, affect productivity, are sensitive to perturbations, and are at risk to contaminant exposure, it is important to understand the effects that anthropogenic perturbations such as the DWH blowout are having on these natural resources. The low temperatures in the deep sea, coupled with the lower organic carbon and nutrient input to deep waters (Montagna et al. 2013), make it likely that hydrocarbons in deepwater sediments will degrade more slowly than in shallow portions of the water column or at the surface. In fact, the half-lives of PAHs in deep waters (>1,000 m) are about twice as long as those in shallow areas (100–150 m), and almost 2.5 times as long as those in the top layer (0–10 m) of the water column (Tansel et al., 2011). The half-life of chrysene in the shallow and deep waters is over 2.5 and about five years, respectively. For pyrene, the half-life in the shallow and deep sediments is about nine and 16 years, respectively. Because of low ambient temperatures, metabolic rates of deep-sea fauna are very low, and life spans and population turnover times are often very long (Baguley et al., 2008; Rowe et al., 2008; Prouty et al., 2016). As a result, recovery of deep-sea communities from the DWH blowout may take decades or longer. ⟳

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