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How Did the Deepwater Horizon Oil Spill Affect Coastal and Continental Shelf Ecosystems of the Gulf of Mexico?

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Tropical spotted dolphins on the West Florida shelf, 2012. *Photo credit: Steven Murawski*

> "Despite the significance of plankton in contributing to the stability of marine food webs, there is surprisingly little pre-Deepwater Horizon baseline information on the seasonal and interannual variability in plankton species composition and plankton dynamics in the northeastern Gulf of Mexico with which to evaluate the impacts of the oil spill."

ABSTRACT. The Deepwater Horizon (DWH) oil spill originated at the base of the continental shelf in the northern Gulf of Mexico (GoM), but large quantities of the oil were transported to the shelf (≤200 m water depth) and into coastal waters (herein defined as ≤15 km from the coast). Water-column effects were generally limited to the period of the ongoing oil releases, although, due to an extensive oil sedimentation event ("dirty blizzard"), effects on the benthos have the potential to be chronic, especially in soft sediments. Impacts on phytoplankton, zooplankton, and ichthyoplankton were relatively short-lived, and the abundance and species composition of planktonic communities returned to pre-spill conditions within a year of the event. Mortalities of larval fish were generally less than 20% of Gulf-wide species populations owing to the extensive and extended spawning periods of most species. Impacts on the productivity of the region's fisheries were also relatively short-lived and influenced by extensive fishery closures to protect seafood safety, although long-term effects may eventually alter the productivity of some stocks.

Benthic communities exhibited effects from the spill that ranged from negligible to significant. Hard-bottom communities, including natural and artificial reefs, suffered injuries that were severe and long lasting. Due to the patchy nature of oil deposition, high tolerance of toxins, and low bioavailability, effects on soft-sediment communities appear to be minimal except in areas, such as beaches, where oil settled in very high amounts. However, DWH oil may persist in coastal and continental shelf sediments for decades if it is sequestered by continuing sedimentation in the absence of events such as tropical storms that may resuspend contaminated bottom material. Nevertheless, vertebrates and shellfish foraging or living in the sediments may be continuously exposed to weathered DWH oil. Understanding the full impacts of the spill requires sustained monitoring in order to separate event-induced impacts from normal variability, and it also requires research that spans the natural range of variation in benthic and pelagic communities. Collection of routine contaminant baselines in GoM waters, sediments, and biota should be viewed as a high priority moving forward.

INTRODUCTION

The Deepwater Horizon (DWH) oil spill originated at the base of the continental shelf in the northern Gulf of Mexico (GoM; McNutt et al., 2012), but large quantities of the oil were transported across the shelf and to coastal waters (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). Because of the complex scenario of oil traversing the water column, surface drift inshore, and sedimentation and sinking of oil and dispersant mixtures, the spill impacted diverse ecosystems and species. In this article we focus on ecosystem effects in the region extending inshore from the continental shelf break to the barrier beaches, bays, and estuaries. We outline the exposure scenario, including the duration and concentration of hydrocarbons in the water column and in bottom sediments, and focus on identified impacts and threats to species and communities potentially vulnerable to these exposure vectors. Planktonic organisms (e.g., phyto-, zoo- and ichthyoplankton) are particularly sensitive to toxic exposures. Given the key ecological roles plankton play in the shelf system, and the fact that many ecologically and economically important invertebrates and fishes spend at least part of their life cycles in the plankton, understanding impacts on them is critical to assessing the DWH spill. Similarly, epifaunal and infaunal invertebrates may be particularly susceptible to DWH impacts because of high rates of sedimentation to the seafloor and subsequent incorporation into the sediment. Furthermore, once associated with sediment, some of the most problematic compounds (e.g., polycyclic aromatic hydrocarbons [PAHs], which are considered persistent organic pollutants) degrade slowly. We also review studies of impacts on coastal and shelf fish communities and fisheries. Finally, we summarize the state of knowledge relative to key ecological questions important for developing more effective oil spill response strategies and recommend enhanced baseline monitoring.

EXPOSURE SCENARIOS IN THE NORTHERN GULF OF MEXICO

The DWH accident released ~4.9 million barrels of oil[1] into the GoM (McNutt et al., 2012). Intensive efforts to collect the discharged oil, and natural processes such as evaporation, reduced the oil in the environment to ~3.7 million barrels (McNutt et al., 2012; Ryerson et al., 2012; Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). About 10% of the total discharged oil formed surface oil slicks covering, at maximum extent in June 19, 2010, over 40,000 km^2 of the ocean (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). Ecosystems were exposed through waterborne oil (short- to medium-term exposures) or through contaminated sediments in the open ocean, along barrier beaches, and in marshes (longer-term and chronic exposures). These two main exposure vectors have unique characteristics, including the duration of exposure, specific oil constituents, and the subset of plants and animals affected by each.

Little has been published on the water-column concentrations of the DWH-derived oil. Therefore, to better describe the water column exposure scenarios for coastal (from the coastline out to 15 km) and continental shelf (from 15 km to the 200 m depth contour) waters, we summarize water-column contamination with data from large public databases available online[2]. The data were collected by BP and US federal agencies from 2010 to 2012, and analyzed for several oil components, including *n*-alkanes (C9-40 and isoprenoids), PAHs (2–6 rings, including alkylated homologs), hopanes (specifically 17α(H)21β(H)-hopane, which is a common forensic standard for oil spills), and BTEX compounds (benzene, toluene, ethylbenzene, and xylenes). These components make up the bulk of crude oil mass. In particular, BTEX and PAH compounds are toxic to marine life. However, the BTEX compounds (primarily occurring in the water column in the DWH scenario) are quickly degraded when released into seawater, whereas PAHs can remain in sediments for many years.

Mean total hydrocarbon concentrations in the water column during summer 2010 (April to August; Figure 1) were 160-fold greater than concentrations measured in years prior to the oil spill (Wade et al., 1989; Mitra and Bianchi, 2003). The largest increase was found for PAHs (up to 4,000-fold increase), followed by BTEX (up to 130-fold increase) and other (aliphatic) compounds (up to 50-fold increase). The highest mean (±95% CI) concentrations were found in the upper 10 m of the water column (total hydrocarbons: 104 ± 17 ppb; PAHs: 43 ± 17 ppb), while intermediate concentrations were found down to 100 m (total hydrocarbons: 22 ± 4 ppb; PAHs: 0.4 ± 0.1 ppb). Lowest concentrations occurred from 100 m to 200 m depth (total hydrocarbons: 7.5 ± 1.8 ppb; PAHs: 0.2 ± 0.1 ppb; Figure 1).

Hydrocarbons in the environment can consist of weathered oil (petrogenic compounds) as well as their combustion products (pyrogenic compounds). Additionally, other naturally occurring hydrocarbons derived from green plants of terrestrial and marine origin may occur. To sort out the sources of hydrocarbons, it is common to use ratios of various hydrocarbon constituents that are typically diagnostic to the source. Using selected hydrocarbon ratios (e.g., the CPI index = ∑odd Cn / ∑even Cn; Pristane/Phytane, PI: ∑(other 3–6 ring EPA priority PAHs) / ∑(5 alkylated PAHs); Retene/Total PAHs; Wang et al., 1999;

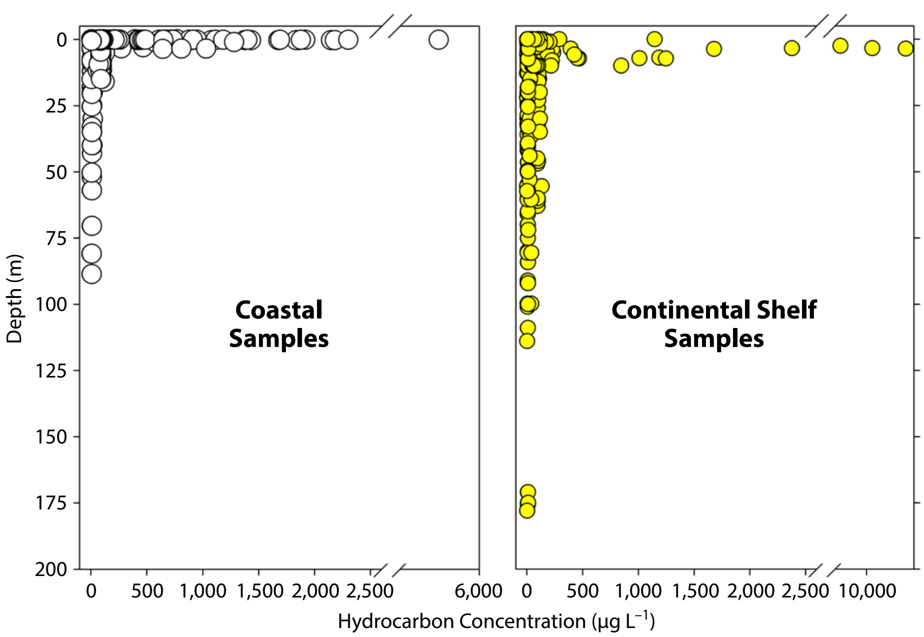

FIGURE 1. Water column profiles of total hydrocarbon concentrations in coastal (N = 2,399) and continental shelf (N = 638) areas in the northern Gulf of Mexico during summer 2010. Total hydrocarbons refers to the sum of *n*-alkanes (C9-40 and isoprenoids), polycyclic aromatic hydrocarbons (PAHs; 2–6 rings polycyclic aromatic hydrocarbons, including alkylated homologs), 17α(H)21β(H)-hopane, and BTEX compounds (benzene, toluene, ethylbenzene and xylenes).

[1] One barrel of crude oil is defined at 42 US gallons. There are approximately 7.33 barrels of oil in one metric ton (MT, depending on the density of the crude oil, which can vary). Thus, the DWH spill resulted in approximately 668,000 MT of oil released or recovered.

[2] http://gulfspillrestoration.noaa.gov; http://gulfsciencedata.bp.com; http://gomex.erma.noaa.gov/erma.html

Romero et al., 2015), we determined that a variety of sources likely contributed hydrocarbons found in the water column during the summer of 2010. On average, 23% of hydrocarbons were from petrogenic and pyrogenic sources (CPI = ~1.0, Retene = < 1%), 24% were from terrestrial sources (CPI > 1.8; PI > 0.30; Retene > 2%), and 47% were from mixed petroleum and terrestrial sources. It is possible that pyrogenic hydrocarbons originated from the incomplete combustion of large surface oil slicks in summer 2010 (~222,000–313,000 barrels were burned) and/or from intense weathering of surface oil slicks exposed to high summer temperatures (25°C–30°C) that enhanced the evaporation of low molecular weight compounds (Ryerson et al., 2012; Romero et al., 2015). Also, these results support the hypothesis that high Mississippi River discharge during the summer of 2010 affected the chemistry of the water column with large inputs of terrestrial-derived dissolved organic matter, sediments, and nutrients that mixed with the spilled oil (Bianchi et al., 2011; O'Connor et al., 2016). In addition, water samples containing hydrocarbon concentrations higher than baseline levels and of petrogenic origin were still found in the water column in 2011–2012 for both coastal and continental shelf areas (total hydrocarbons: 8.6 ± 1.1 ppb; PAHs: 1.1 ± 0.5 ppb; BTEX: 2.3 ± 0.01 ppb). This suggests resuspension of the deposited hydrocarbons after summer 2010 promoted long-term presence of DWH-derived hydrocarbons in the water column of the study area (Turner et al., 2014).

To estimate the excess concentration of hydrocarbons in the water column in summer of 2010 due to DWH (i.e., referenced against baseline concentrations), depth-integrated hydrocarbon values were calculated for each profile and averaged by month. Spatial interpolation of these water-column data (empirical Bayesian kriging analysis modified from Valentine et al., 2014, and Chanton et al., 2015) indicates that 40,692 km^2 in the coastal area and 103,500 km^2 in the continental shelf area were contaminated (e.g., excess hydrocarbon concentrations >0; Figure 2). The concentrations of PAHs exceeded levels generally thought to induce impacts to marine life (>17.9 µg L^{-1}; Heintz et al., 1999; Hoff et al., 2010) in 88% of coastal and continental shelf areas.

The estimated quantity (±95% CI) of hydrocarbons in the water column for one month in summer of 2010 (minus baseline concentrations) was 15,428 ± 2,080 MT in coastal areas and 145,467 ± 63,038 MT on the continental shelf. Based on the hydrocarbon source ratios, oil-derived hydrocarbons account for ~23% (or 36,465 MT) of the total amount of hydrocarbons in the water column (~160,895 MT). The remaining ~77% (or 124,430 MT) is predominantly of terrestrial and mixed sources, indicating a larger impact of the Mississippi River system on water-column processes during the DWH oil spill than previously described in more spatially restricted studies (Bianchi et al., 2011; O'Connor et al., 2016). Relative to the DWH spill, oil-derived hydrocarbons accounted for 15 ± 2% (or 5,930 ± 959 MT) in the coastal area and 75 ± 45% (or 30,535 ± 18,392 MT) on the continental shelf of the total oil discharge from DWH (~40,857 MT of saturated, aromatic, and BTEX fractions for one month of the spill; Reddy et al., 2011).

Overall, our calculations indicate that contamination occurred in 144,192 km^2 of the northern GoM coastal and continental shelf areas, an estimate larger than previously reported for the cumulative oil slick coverage (~111,000 km^2; Figure 3) and the deep seafloor covered

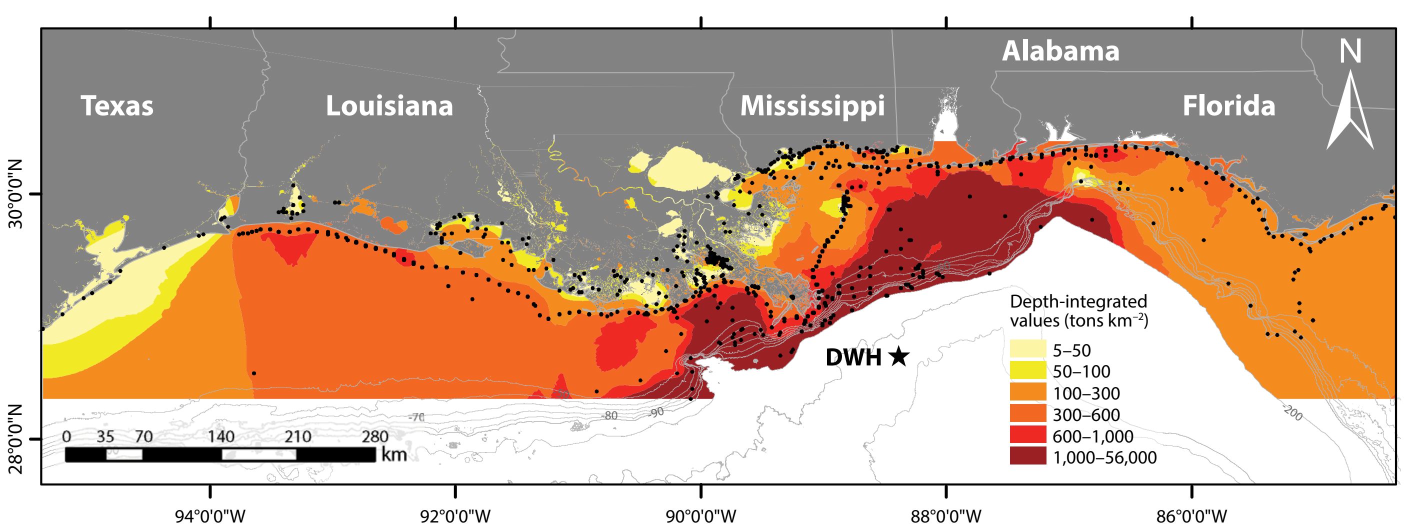

FIGURE 2. Spatial interpolation of water column hydrocarbon concentrations (minus background) in coastal and continental shelf areas in the northern Gulf of Mexico. Data are shown as depth-integrated concentrations of samples (N = 2,759) collected in summer of 2010 (April to August). Hydrocarbons refers to the sum of *n*-alkanes (C9-40 and isoprenoids), PAHs (2–6 rings polycyclic aromatic hydrocarbons, including alkylated homologs), 17α(H)21β(H)-hopane, and BTEX compounds. Data were interpolated using empirical Bayesian kriging analysis, including the regions where few samples were taken (e.g., continental shelf off of Texas and western Louisiana). The star indicates the location of the Deepwater Horizon (DWH).

by DWH oil (~1,030 km^2; Valentine et al., 2014; Chanton et al., 2015; Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016).

With respect to contamination of GoM sediments, a number of published studies indicate that a substantial proportion of DWH oil was transported to the seafloor (Schwing et al., 2014; Valentine et al., 2014; Brooks et al., 2015; Chanton et al., 2015; Romero et al., 2015; Daly et al., 2016). Because so much DWH oil was located in the water column above the continental shelf and in coastal areas, it is likely that the sediments in these areas contain substantial quantities of sedimented oil as well, although at concentrations likely higher than the deep areas adjacent to the well. Sedimented hydrocarbons represent exposure vectors to benthic communities, just as water-column concentrations expose pelagic organisms to potential spill-related impacts.

IMPACTS ON PHYTOPLANKTON AND ZOOPLANKTON

Phytoplankton and zooplankton play critical roles in mediating the structure of pelagic communities and sustaining fisheries. Zooplankton constitute a dominant prey item for larval as well as some adult fishes, and most economically and recreationally important shellfish and fish species spend their earliest life stages as members of the zooplankton community. Despite the significance of plankton in contributing to the stability of marine food webs, there is surprisingly little pre-DWH baseline information on the seasonal and interannual variability in plankton species composition and plankton dynamics in the northeastern GoM with which to evaluate the impacts of the oil spill. Because of the duration and concentration of oil in the water column, the DWH spill was responsible for a variety of mostly short-term impacts on the planktonic community of the northern Gulf.

The northeastern GoM in the area of the DWH oil spill is a relatively productive region (Lohrenz et al., 1997). The major physical processes influencing pelagic ecosystems are seasonal changes in surface temperature, winds, river discharge, and circulation features, such as shelf slope eddies, the Loop Current and its eddies, and storms. The linked Mississippi and Atchafalaya Rivers are the primary source of nutrient-rich water, followed by the Tombigbee and Alabama Rivers that empty into Mobile Bay, and the Apalachicola River in Northeast Florida; thus, these rivers exert a major control on the timing and magnitude of primary production (Jochens et al., 2002). During the DWH oil spill, freshwater diversions along the lower Mississippi River were opened between mid-May and October with the intent to minimize the impact of the oil spill on estuaries and wetlands (Bianchi et al., 2011). In addition to wind forcing, Mississippi River-induced circulation significantly influenced near-surface oil transport (Kourafalou and Androulidakis, 2013). Three storm events during the oil spill led to changes in surface oil extent and deep mixing and likely nutrient injection into surface waters (Goni et al., 2015). Sampling stations in the vicinity of DeSoto Canyon were occupied between August 2010 and August 2014 to collect hydrographic data, nutrients, chlorophyll, and zooplankton (Figure 3). Surface chlorophyll values for these stations ranged from 0.78 μg L^{-1} to 2.00 μg L^{-1}, and the dominant phytoplankton were diatoms, with *Thalassionema nitzschiodes*, *Pseudonitzschia* spp., and *Dactyliosolen fragillissimus* densities ranging from 11,000 cells L^{-1} to 364,000 cells L^{-1}. In contrast, August 2012 had lower river flow, surface salinities were higher, and chlorophyll concentrations were lower (0.10–0.26 μg L^{-1}).

Paul et al. (2013) report that phytoplankton and bacteria were still exhibiting toxic and mutagenetic effects from oil and dispersants at off-shelf sites after the wellhead was capped in July 2010 (Figure 3). Samples collected during and after the

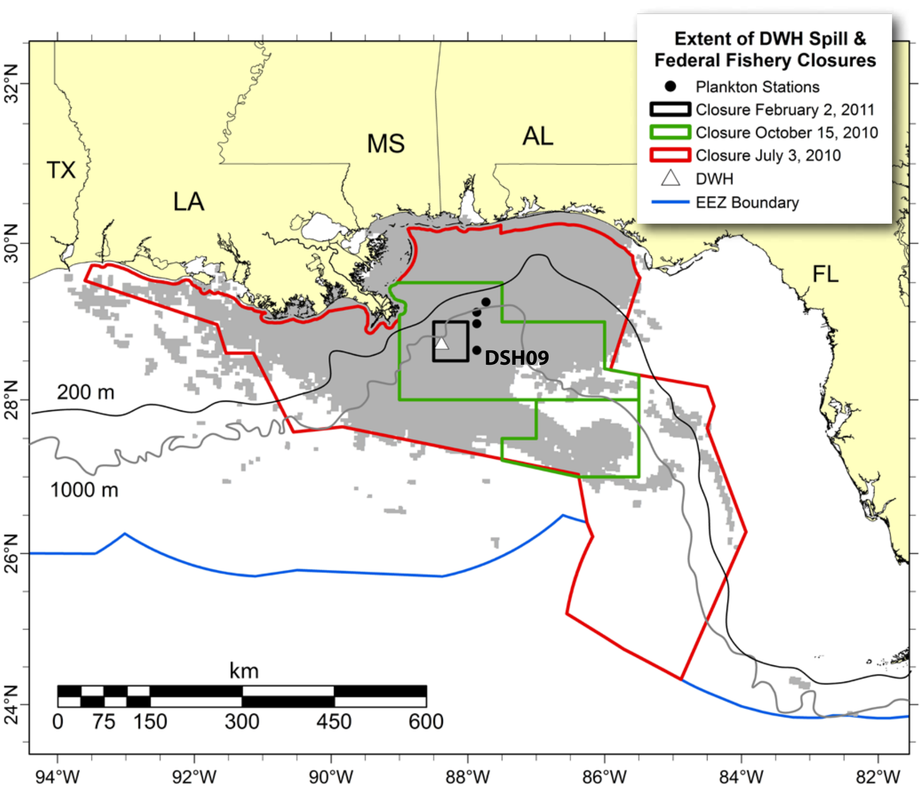

FIGURE 3. Cumulative distribution of surface oil as observed from satellites (gray shading), and the spatial extent of federal fishery closures on July 3 and October 15, 2010, and February 2, 2011 (SERO, 2015). Station locations for hydrographic data, chlorophyll, nutrients, marine snow, and zooplankton abundance (see Figure 5) are indicated as black circles.

DWH oil spill (May–October 2010) on the Louisiana shelf west of the Mississippi River indicate that phytoplankton abundances were 85% lower compared to baseline data collected during the previous 20 years, primarily due to a decline in phytoflagellates (Parsons et al., 2015). Overall, phytoplankton species composition shifted toward diatoms, dinoflagellates, and cyanobacteria, whereas autotrophic ciliates, phytoflagellates, and coccolithophorids were not observed in 2010. On the other hand, heterotrophic microzooplankton biomass was similar to values reported in previous years and, therefore, probably did not account for the decline in phytoflagellates. An increase in heterotrophic cilates and zooflagellates indicates that bacterial densities likely increased.

In contrast to the results on the Louisiana coast, Hu et al., (2011) and O'Connor et al. (2016) reported an anomalous phytoplankton bloom north of the DWH spill location during August 2010, based on satellite-derived ocean color observations (Figure 4). Based on historical satellite data, the intensity and location of this anomaly were unusual, as normalized fluorescence line height (nFLH, a relative measure of surface biomass) derived from the measurements of the Moderate Resolution Imaging Spectroradiometer (MODIS) reached a maximum as compared with any August before or after 2010. The MODIS-derived surface chlorophyll concentration in the vicinity of the anomaly also showed that the bloom intensity was at least twice that of normal spring blooms. Although there is some degree of uncertainty in such estimated chlorophyll concentrations due to interference of colored dissolved organic matter from coastal runoff (Hu et al., 2003), the relative temporal patterns should be valid. There are several possible explanations for the elevated chlorophyll concentrations, including nutrient enhancement from runoff of terrestrial origin (O'Connor et al., 2016) or some factor related to the DWH oil spill (Hu et al., 2011), as coastal runoff alone did not appear to be sufficient to lead to the large anomaly. Indeed, historical data collected in the vicinity of the DWH spill showed lower chlorophyll levels than presented here in a similar salinity range (Nababan et al., 2011), suggesting an additional factor leading to the elevated chlorophyll. It is, however, unclear how an oil spill could induce an increase in nutrients.

During August 2010, there was an unexpected extended sedimentation event of oil-associated marine snow (Daly et al., 2016). The formation of marine snow, incorporation of oil into it (called marine oil snow), and its subsequent settling to the seafloor has become known as MOSSFA (marine oil snow sedimentation and flocculant accumulation). This mass deposition of marine oil snow to the seafloor was primarily a product of marine snow formation and appears to have occurred over a four to five month period during and after the oil spill, far exceeding pre-spill sediment accumulation rates (Brooks et al., 2015). Thus, this sedimentation event was a significant pathway for the distribution and fate of DWH oil, accounting for 4% to as much as 14% of the total oil released (Chanton et al., 2015).

Marine snow consists of particles >0.5 mm to tens of centimeters in size, including aggregations of small inorganic particles, bacteria, phytoplankton, microzooplankton, zooplankton fecal pellets, larvacean houses, terrestrially derived lithogenic components, and detritus (Passow and Ziervogel, 2016, in this issue). Phytoplankton and bacteria release "sticky" exopolymeric substances (EPS) as a result of exposure to oil and dispersant, and this mucus acts as a glue, providing the matrix for aggregates (Passow and Ziervogel, 2016, in this issue). Even though these large mucus particles had disappeared by June (Passow et al., 2012), smaller marine snow particles were still relatively abundant into August (Daly

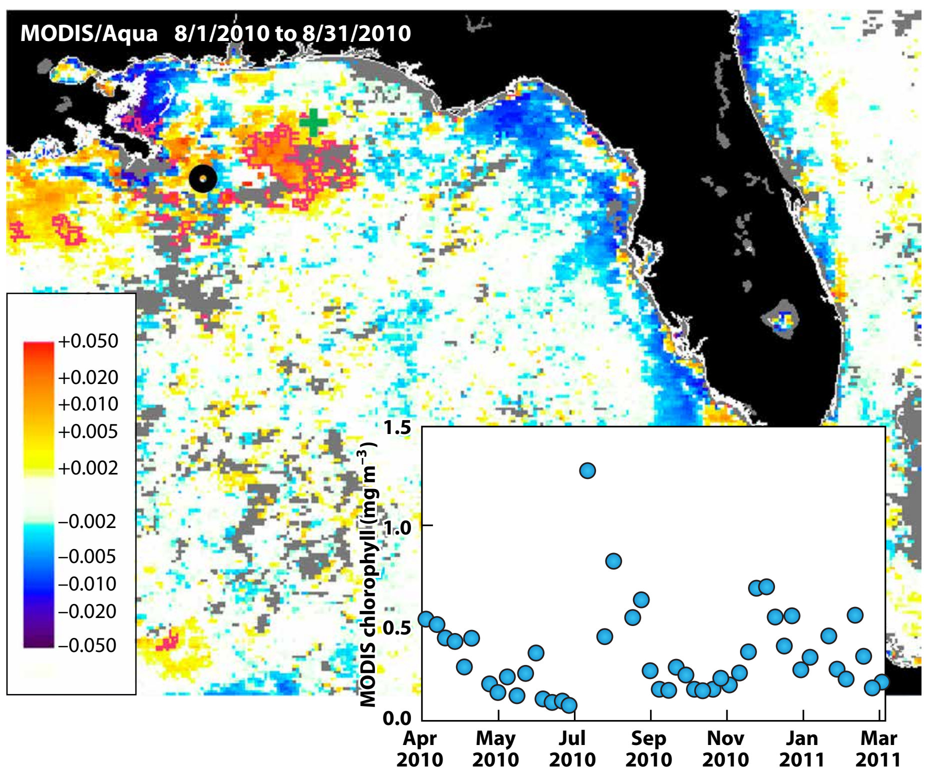

FIGURE 4. Moderate Resolution Imaging Spectroradiometer (MODIS) image normalized fluorescence line height (nFLH in mW cm^{-2} μm^{-1} sr^{-1}) anomaly during August 2010 (Hu et al., 2011). Statistically significant anomaly is annotated by the pink outline. The Deepwater Horizon site is marked with a black circle, while a sediment core site at 29°24'N, 86°46'W is marked with a green plus sign. The inset graph shows the MODIS-derived surface chlorophyll concentrations at the sediment core site between April 2010 and March 2011.

et al., 2014, 2016). A times-series site (DSH09) 50 km east of the DWH wellhead (Figure 3) provided information on the interannual variability of the abundance and vertical distributions of marine snow off the shelf edge (Figure 5). Integrated marine snow concentrations between 0 m and 100 m during August 2010 were considerably higher than during September 2011, August 2012, August 2013, or August 2014. Marine snow concentrations were highest during the oil spill and during August 2013, another relatively high river flow year.

Carassou et al. (2014) reported that zooplankton (calanoid and cyclopoid copepods, ostracods, bivalve larvae, and cladocerans) collected at several time-series inner-shelf stations near the mouth of Mobile Bay showed significantly higher densities during May and June 2010 compared to historical levels, but not during July 2010. Thus, the impact of the DWH oil was short-lived, and recovery was rapid at this location. There are currently no historical zooplankton data that can be used to evaluate impacts on off-shelf zooplankton. However, post-oil-spill data show a similar pattern to nearshore sites. Off-shelf zooplankton abundance (integrated 0–100 m) to the east of the DWH wellhead in the vicinity of DeSoto Canyon (Figure 5) was relatively high during August 2010, within one month after the wellhead was capped, compared to the following four summer periods (Figure 5). In general, zooplankton abundances were higher during years of high river flow and higher chlorophyll concentrations (2010, 2013) and lower during intermediate or low river flow years (2011, 2012, 2014). Although plankton community abundance levels have not shown a negative long-term impact from the oil spill, shifts in species composition are still being evaluated. Complex, nonlinear food web effects may still occur due to the transfer of bioaccumulated hydrocarbons from zooplankton to higher trophic level predators. Also, very little is known about the long-term effects of toxins at the molecular level of organisms. During the DWH oil spill, oil carbon was incorporated into the lower trophic food web through biodegradation by bacteria (Graham et al., 2010; Cherrier et al., 2013; Chanton et al., 2015). Bioaccumulation of hydrocarbons by the planktonic food web would increase exposure of higher-trophic-level organisms.

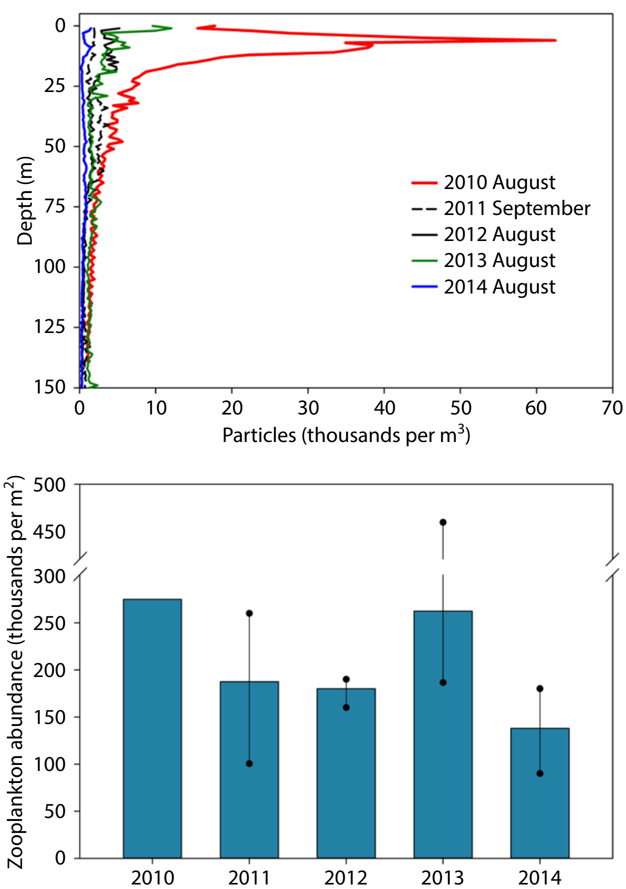

FIGURE 5. (top) Vertical distributions of marine snow concentrations (thousands of particles per m^3) during August 2010 at Station DSH09 (see Figure 3 for location), compared to vertical profiles of marine snow during the following four summers. (bottom) Total zooplankton abundance (numbers, in thousands per m^2) integrated between 0 m and 100 m depth for August 2010, September 2011, August 2012, August 2013, and August 2014. Data were collected by the SIPPER camera imaging system at stations off shelf to the east of the Deepwater Horizon site (see Figure 3). Abundances are the geometric means of four to five stations, except for 2010 when data were only collected at one station (DSH09); black bars are minimum and maximum integrated zooplankton concentrations.

IMPACTS ON THE BENTHOS

Relatively few studies were conducted on oiled beaches following the DWH event, even though risk analysis indicated beach and intertidal fauna would be severely impacted (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). Bik et al. (2012) applied molecular techniques to examine the eukaryotic benthic community at beaches around Mobile Bay, Alabama, in May 2010 before oil reached the shore and again in September 2010 after oiling had occurred. Nematodes were the most abundant taxon before oiling but were greatly reduced in abundance after oiling when fungi became dominant. Brannock et al. (2014) sampled the same beaches in 2011 and 2012 with the same molecular techniques and observed that fungi had become rare while nematodes and other animal taxa increased in abundance. Thus, the post-spill dominance of fungi on oiled beaches was short-lived, and a more typical metazoan community was found approximately one year after oiling.

The relatively few studies conducted in response to the spill along the coast or on the continental shelf examined soft-sediment as well as hardbottom communities. In soft sediments, Landers et al. (2014) sampled the meiobenthos in 2012 in areas as close as 54 km from the blowout site and found that diversity and abundances were high and similar to those found in pre-spill collections.

No correlation between meiofaunal density and sediment contaminants was observed. Cooksey et al. (2014) surveyed macroinfauna at 50 stations positioned randomly across the shelf at depths from ~10 m to the shelf break in August 2010. The blowout site was 30 nautical miles (~55 km) from the nearest station, and sampling stations included areas where there were large or near-continuous surface oil slicks. Sediment PAHs were found at levels typical of regional background contamination, and were much lower than concentrations indicative of negative effects based on sediment-quality guidelines. No spill-related impacts on abundances or species diversity were detected in these studies.

Two very different hardbottom communities at ~50–75 m water depths were compared using pre- and post-spill monitoring data. One community exhibited encrusting algae and associated fauna found on rhodoliths (unattached calcium carbonate nodules), and the other was associated with mesophotic reefs (which are characterized by the presence of light-dependent corals under low-light conditions). Felder et al. (2014) reported that the diversity and abundance of macroalgae and decapod crustaceans associated with rhodoliths decreased dramatically after the spill. Their study sites were >100 km from the wellhead and were only intermittently or sporadically exposed to surface oil, and the authors caution that their sites could have been affected by other environmental perturbations during the sampling period. Observations based on comparisons to video collected before the spill on Pinnacle Reefs (mesophotic reefs comprising approximately 16 km^2 of the seabed near the shelf break off Mississippi and Alabama) indicate acute spill-related mortality, especially for corals and tall-form sea fans (Etnoyer et al., 2015; Silva et al., 2016). Approximately one-third to one-half of large sea fan colonies were injured in 2011, and spill-related injuries to Pinnacle Reefs have persisted for at least four years and may persist for much longer (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016).

IMPACTS ON FISH AND FISHERIES

The GoM region is home to a highly diverse community of fishes comprised of nearly 700 species, constituting over 300 genera and 84 fish families (McEachran and Fechhelm, 2005). Reflecting this diversity, the region's fisheries are likewise supported by an array of species, including oceanic pelagic species (tunas, billfishes, dolphinfish), coastal pelagics (menhaden, mackerels), shelf demersal fishes including snappers and groupers, and inshore species including drums and croakers, and important invertebrate fisheries for shrimps (white, brown, pink), blue and stone crabs, spiny lobster, and American oyster.

Concern for the integrity and safety of the seafood supply during the DWH spill prompted federal and state officials to institute fishery closures (Figure 3; Ylitalo et al., 2012). Closures in federal waters expanded in size and scope as the surface oil expanded, at one point covering about 290,000 km^2, or about one-third of the US Exclusive Economic Zone (EEZ) in the GoM (Figure 3). Testing of fish muscle for PAHs and organoleptic sampling was conducted with fish from closed areas, and negative tests resulted in a phased reopening, with most areas opened by November 2010 (Figure 3; Ylitalo et al., 2012).

Fishery closures in 2010 had a significant but in most cases short-term impact on catches (Figure 6). Overall commercial fishery landings (MT) declined by 25.3% from 2009 to 2010, with finfish, shrimp, oyster, blue crab, and menhaden landings declining by 24.4, 28.7, 30.1, 32.7, and 24.9%, respectively. Importantly, the value of the landings declined by only 1.8% between 2009 and 2010, with shrimp value (the highest value GoM fishery) actually increasing 3.6% between 2009 and 2010. Subsequent to the spill, overall landings and value of GoM fisheries between 2010 and 2014 increased 6.6% and 64.5%, respectively. The value of GoM commercial fisheries in 2014 was $1.03 billion (first sale value), with strong increases in the prices for shrimp, oyster, and blue crab driving increases in recent years. During 2010, the states most affected by the spill were Mississippi (−51.7% MT, −42.4% value), Alabama (−51.0% MT, −33.6% value), and Louisiana (−21.3% MT, −18.6% value). Least affected were Texas (−12.3% MT,

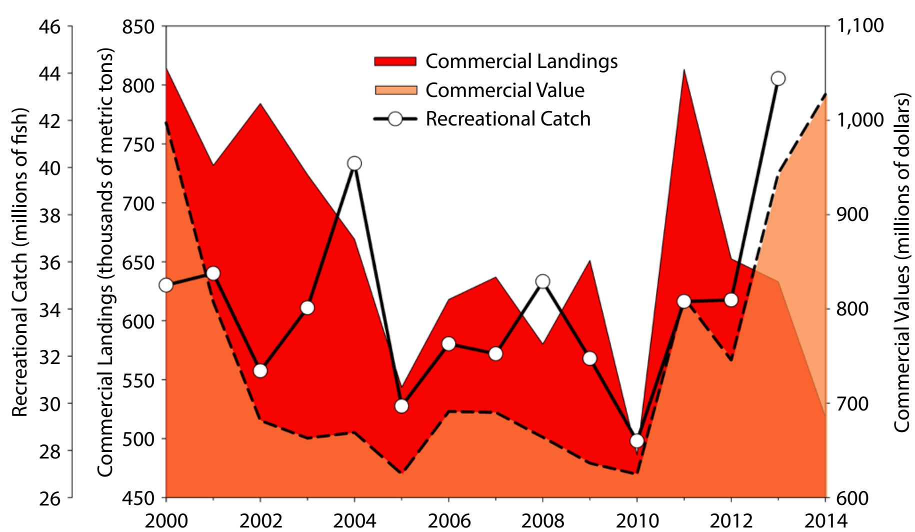

FIGURE 6. Gulf of Mexico commercial fishery landings (thousands of metric tons), commercial fishery values (millions of dollars), and recreational fishery catches (landings + live discards in millions of fish), 2000–2014. Recreational data are from NMFS (2015).

+31.9% value) and Florida (−4.0% MT, +19.4% value). Since 2010, landings and their values have returned to pre-spill levels or greater for most fishery species (Figure 6). Recent declines in total fish landings are driven by reduced catches of menhaden, which can be highly variable from year to year (Figure 6). Recreational fisheries catches (landings plus discarded live fish) declined 11% Gulf-wide between 2009 and 2010, but have since risen steadily to a 15-year time-series high in 2013 (Figure 6).

While GoM fisheries landings declined in the short term, and returned to pre-spill levels in one to two years following the spill, changes in the productivity of stocks due to oil spill effects at the population level may take several to many years to manifest, owing to the specific life histories of target animals. Short life cycle species (e.g., shrimps, oysters, crabs) can rebound quickly, as long as the reproductive capacity of the species is maintained. Longer-lived species (e.g., bluefin tuna, red snapper, some groupers), and particularly those with distributions centered within the oil spill range, may suffer longer-term declines if year class strength or growth rates are impaired. Below, we summarize currently available information about impacts on fish communities, focusing on larval-phase exposure, toxic effects on population-level productivity, and longer-term fish community change.

Early Life History Impacts

In order for an oil spill to have significant population-level effects on the early life history of fishes, at least three important conditions must be met: (1) exposure to oil results in adverse effects including increased mortality and reduced fitness of animals exposed, (2) observed concentrations in nature are sufficient to cause increased mortality and sublethal impairment, and (3) a substantial fraction of the population is exposed to critical levels of oil in the environment. Laboratory studies conducted before and since DWH have emphasized the vulnerability of fish larvae to even minute levels of oil exposure (1–2 ppb). For example, Incardona et al. (2014) demonstrate that exposure of bluefin tuna, yellowfin tuna, and an amberjack larvae exposed in laboratory trials to ΣPAH concentrations of 1–15 μg L^{-1} (ppb) caused defects in cardiac function likely leading to mortality and morbidity. Similarly, dolphinfish eggs and larvae exposed to mean (±95% CI) ΣPAH concentrations of 1.2 ± 0.6 to 30 ± 7 μg L^{-1} ΣPAHs exhibited reduced swimming performance and associated cardiac abnormalities, presumably leading to increased mortality (Mager et al., 2014). Findings of elevated mortalities from exposures in this range are documented among many taxa (e.g., Heintz et al., 1999). Thus, the first condition for population-level impacts owing to PAH exposure as noted above is met. With respect to the critical concentrations of PAHs in nature resulting from DWH, our findings (see section on Exposure Scenario in the Northern Gulf of Mexico above; Figure 2) indicate a substantial proportion of the water column had elevated PAH concentrations associated with the spill: averaging 43 μg L^{-1} in the upper 10 m, 22 μg L^{-1} in waters <100 m, and 7.5 μg L^{-1} in 100–200 m water depth (Figure 1). In all cases, these average concentrations were sufficient to elicit negative physiological effects consistent with laboratory exposures. Thus, the second condition is also met.

The question remains as to what fraction of various species populations was potentially exposed as larvae to elevated PAH scenarios from DWH. Using ichthyoplankton data collected in standardized Southeast Area Monitoring and Assessment Program (SEAMAP) surveys from 1982 to 2009, Chancellor (2015) computed the fraction of larvae occurring within the spatial (Figure 2) and temporal (April–July) bounds of the active spill for 110 taxa of identified larvae. These fractions ranged from 0% to 28.6% of the total larvae in the northern GoM, depending on the taxon. The spatial overlap with the oil spill included a number of commercially and recreationally important species such as cobia (22.5%), spotted seatrout (28.6%, oceanic distribution only), bluefin tuna (14.5%), red snapper (5%), dolphinfishes (12.5%), Spanish mackerel (13.9%), and non-fishery species such as anchovies (24.3%) and myctophids (14.5%). Because of the widespread distribution and extended spawning periods of most species and relatively high larval transport/dispersal, the third condition for significant population-level effects of the spill are only partially met, as the fractions of total larval production exposed to the oil spill were low to modest.

Impacts on Fish Recruitment

Potential impacts on recruitment of fishes have long-term implications for stock productivity. Recruitment impacts can result from direct mortality on early life stages (e.g., egg and larval exposure leading to death), from juveniles either exposed directly or through tainted food, or from cascading ecosystem impacts (e.g., through depletion of critical phyto- or zooplankton food sources at critical periods in the life cycle). Longer-term concerns for the health of exposed fish populations are genotoxic impacts that may alter the survivability or growth of stocks.

There is some evidence that the eastern GoM red snapper substock may have exhibited recruitment declines post-2010 (SEDAR, 2013; Herdter, 2014; Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). Relatively low abundances of juvenile red snapper were observed in SEAMAP surveys in the eastern GoM in 2010 and 2011. Reduced catch rates for small (<500 mm) and young (<5 years) red snapper in the eastern GoM resulted in lower recruitment estimates for the eastern versus the western GoM in the years following the DWH spill (SEDAR, 2013). While a positive trend in spawning stock biomass (SSB) that began prior to DWH continues for the western GoM substock, declines in small, young fish in the eastern GoM translate to declining SSB in that substock. However, uncertainty

FIGURE 7. Sampling fishes and for sediment cores aboard R/V *Weatherbird II*. (left) Members of the Murawski Lab (top left Kristina Deak, Erin Pulster, Elizabeth Herdter, Susan Snyder; lower left Steve Murawski, Amy Wallace) at the University of South Florida with a catch of yellowedge grouper sampled off the Louisiana coast, 2015. (top right) Sediment multicorer being deployed from the ship. (lower right) Susan Snyder and Kristina draw blood from a red snapper for immune-toxicological studies. *Photo credits: Shannon O'Leary*

remains as to whether DWH effects or other coincident environmental factors drove observed declines in recruitment (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016).

Community-Level Impacts

A number of studies document changes in fish communities in northern GoM shelf communities by integrating pre- and post-spill abundance levels, trophic structure, and species diversity. Significant changes in the abundance of some species and in trophic structure occurred on natural and artificial reefs on the continental shelf, including shifts in red snapper and tomtate diet and trophic position following the spill (Norberg, 2015; Tarnecki and Patterson, 2015). Both red snapper and tomtate displayed diet shifts to higher trophic position prey that was corroborated by higher $\delta^{15}N$ values in the first two years following the DWH spill. These species also displayed shifts to more benthic versus pelagic prey, which were associated with a general decline in small demersal fishes, such as damselfishes (Kristen Dahl, University of South Alabama, *pers. comm.*, 2016). Analysis of stable carbon and radiocarbon isotopes in reef fish muscle tissue indicates that these trophic shifts occurred at the same time that petrocarbon (depleted ^{13}C and ^{14}C signatures), likely from the DWH spill, reached the level of fishes in the food web (Norberg, 2015; Tarnecki and Patterson, 2015).

Interpretation of reef fish community shifts following the DWH spill are potentially confounded by recent colonization by invasive lionfishes (Dahl and Patterson, 2014), as well as by fishery closures on the shelf in summer 2010. Lionfish were first observed in the northern GoM in the summer of 2010, and their population levels have expanded exponentially since then (Dahl and Patterson, 2014; Kristen Dahl, University of South Alabama, *pers. comm.*, 2016). However, declines in small demersal reef fishes of >90%, as well as declines in large piscivores such as snappers and groupers of >50%, were apparent by fall 2010 when lionfish were first observed in the northern GoM (Dahl and Patterson, 2014; Kristen Dahl, University of South Alabama, *pers. comm.*, 2016). Therefore, it is unlikely lionfish caused the initial shifts in reef fish community structure observed following the DWH spill. A more plausible scenario is that the overall declines in native reef fish biomass and diversity following the DWH spill lowered biological resistance in the system, thus enabling lionfish to invade the northern GoM region quicker, and reach higher densities, than any other part of their invaded range in the western Atlantic (Dahl and Patterson, 2014; Chagaris et al., 2015).

In the case of reef fishes, abundances of exploited species actually declined by approximately 25%–50%, as estimated with remotely operated vehicle surveys across the shelf from 2009 to 2015 (Kristen Dahl, University of South Alabama, *pers. comm.*, 2016). It should be noted that this pattern contrasts with that reported for some inshore fish populations in which no declines, or even increases, in some species were reported (Fodrie et al., 2014; Schaefer et al., 2016).

> “While Gulf of Mexico fisheries apparently declined in the short term, and returned to pre-spill levels in one to two years following the spill, changes in the productivity of stocks due to oil spill effects at the population level may take several to many years to manifest, owing to the specific life histories of target animals.”

SUMMARY AND DISCUSSION

The addition of nearly 700,000 MT of crude oil from the DWH oil spill had measurable and significant impacts on the coastal and continental shelf environments of the northern GoM. The DWH volume was about seven times the normal yearly “oil budget” of the entire GoM (National Research Council, 2003; Murawski et al., 2014), over a compressed time interval of 87 days (McNutt et al., 2012), resulting in an estimated 160-fold increase in water column total hydrocarbon concentration during April–July, 2010. Much of the region had water column concentrations of PAHs that are generally thought to induce negative impacts to marine life (i.e., >17.9 µg L^{-1}).

Published studies and data analyzed herein confirm the significant but ephemeral nature of water-column effects in coastal and continental shelf areas (Figures 4 and 5), most of which declined quickly and substantially after the well was closed. Nevertheless, the toxicity of oil and dispersants in the water column likely induced phytoplankton to produce large quantities of EPS. The opening of water diversion structures resulted in substantial increases in freshwater discharges, carrying increased nutrient and fine sediment loads to the coastal ocean. Thus, all of the elements necessary for a massive marine oil snow event, a so-called dirty blizzard, were in place: large quantities of dead plankton, increased nutrients stimulating increased productivity in the region where toxic oil was located, fine sediments to ballast aggregates to the bottom, and large quantities of EPS to bind and ultimately sink the plankton, oil, and sediments. Evidence of mass sinking marine oil snow and its accumulation in sediments is discussed in Passow and Ziervogel (2016, in this issue).

Water-column effects on phytoplankton and zooplankton productivity and species composition were short-lived, with productivity returning to pre-spill levels quickly after the spill (Figure 5). Northern GoM plankton productivity is dominated by effects of freshwater discharges, which occur aperiodically. Impacts of DWH on the planktonic communities are thus difficult to judge against this variability. With respect to ichthyoplankton, during the period April to July, many of the GoM’s fish species spawn in order to take advantage of increased zooplankton abundance in the spring, associated with seasonal runoff and productivity cycles. Spawned eggs generally hatch in about one day, but larvae may persist in the water column for a month or more, depending on the species, increasing their probability of interacting with oil. Despite concerns about larval impacts on depleted western bluefin tuna stock spawning in the GoM, only an estimated 12%–14% of larval production (Muhling et al., 2012; Chancellor, 2015) occurred in the spill zone. Similarly, only about 5% of red snapper larval production was potentially exposed, although a larger proportion of the eastern GoM substock may have been affected. Given natural variation in egg and larval mortality in the majority of fish stocks, these levels are likely indistinguishable against a background of natural variability in recruitment.

DWH oil spill impacts on benthic ecosystems in coastal and shelf areas are diverse and complex. A substantial proportion of DWH oil sedimented to the seafloor (Schwing et al., 2014; Brooks et al., 2015; Romero et al., 2015; Valentine et al., 2015; Chanton et al., 2015; Daly et al., 2016). Concentrations in shelf sediments were most problematic in coastal areas, especially east of the Mississippi River, although few post-spill benthic samples were collected in this region. Oil input to the seafloor was episodic over much of the deeper shelf, and low bioavailability associated with muddy sediments likely reduced exposure to levels that would not cause toxicity to most infauna (Cooksey et al., 2014). However, burrowing fishes at the shelf edge, such as tilefish, exhibited relatively high and persistent levels of bile metabolites of PAHs, indicative of oil exposure (Murawski et al., 2014; Snyder et al., 2015), but this effect was species-specific, probably owing to differing physiology and metabolic pathways among them. Hardbottom benthos (including macroalgae, crustaceans, mollusks, and corals) associated with natural and artificial reefs were exposed to oil as it settled to the seafloor, and effects were likely acute, widespread, and persistent because of higher exposures or lower tolerance. For example, strong and persistent effects were observed on mesophotic reef communities (Etnoyer et al., 2015; Silva et al., 2016). Unlike water-column effects, impacts on benthos and benthic-foraging populations may be persistent, chronic, and problematic for some communities, but they were not universal across the continental shelf, due at least in part to the patchy nature of oil deposition. Furthermore, oil may persist in association with sediments for very long periods of time (e.g., decades), and it is possible that sequestered oil could chronically affect benthos and foraging or burrowing fish and shellfish, at least in areas of the shelf not subject to seafloor suspension associated with fronts and tropical storms.

The region's fisheries were impacted due to extensive fishery closures in 2010 as well as health effects on some species, but they quickly rebounded thereafter (Figure 6), although long-term health effects may alter the productivity of some stocks. Ironically, the short-term fishery closures associated with the spill may have enhanced productivity of some short-lived stocks (Schaefer et al., 2016), pointing to the pervasive effects of fishing in the Gulf of Mexico. As with the *Exxon Valdez* spill, many of the effects of DWH may take a decade or more to become apparent. With respect to fish populations affected by *Exxon Valdez* in Prince William Sound, impacts have specifically focused on Pacific herring (Thorne and Thomas, 2008) and pink salmon (Heintz et al., 1999). In both fish species, unlike with DWH, a substantial fraction of the egg and larval production of the affected substocks occurred within the spill zone. In addition, these stocks may have suffered from chronic exposure of multiple cohorts from weathered oil sequestered in sediments where the demersal eggs of these species were deposited (Peterson et al., 2003).

Assessing the aftereffects of DWH has highlighted important and ongoing gaps in our knowledge. Prior to the spill and even now, there is no comprehensive baseline of oil contamination in the GoM's sediments, water column, or biota. Most US oil and gas infrastructure exists west of the DWH site (Figure 3), outside the area where most DWH-related studies were undertaken. Should a large spill occur west of the Mississippi River, there would again be no suitable baseline in coastal and shelf waters to use to separate background from exposure. While ecosystems of the northern GoM have adapted to persistent low levels of hydrocarbons, the addition of massive amounts in a short time obviously exceeded critical tipping points for sensitive communities. Understanding these critical thresholds starts with better knowledge of the contamination baselines and of the natural variability of planktonic and benthic communities. The economic importance of the GoM's hydrocarbon and living marine resources to the region and the nation justifies sustained investment in monitoring and assessment to better understand the impacts of multiple human activities, including accidental releases of oil and responses to them.

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