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Environmental effects of the Deepwater Horizon oil spill: A review

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Abstract

The Deepwater Horizon oil spill constituted an ecosystem-level injury in the northern Gulf of Mexico. Much oil spread at 1100-1300 m depth, contaminating and affecting deepwater habitats. Factors such as oil-biodegradation, ocean currents and response measures (dispersants, burning) reduced coastal oiling. Still, >2100 km of shoreline and many coastal habitats were affected. Research demonstrates that oiling caused a wide range of biological effects, although worst-case impact scenarios did not materialize. Biomarkers in individual organisms were more informative about oiling stress than population and community indices. Salt marshes and seabird populations were hard hit, but were also quite resilient to oiling effects. Monitoring demonstrated little contamination of seafood. Certain impacts are still understudied, such as effects on seagrass communities. Concerns of long-term impacts remain for large fish species, deep-sea corals, sea turtles and cetaceans. These species and their habitats should continue to receive attention (monitoring and research) for years to come.

Key words: Deepwater Horizon oil spill; environmental effects; review

1. Introduction

On April 20th 2010, an explosion on the Deepwater Horizon (DWH) drilling rig led to a catastrophic oil and gas blowout at the BP operated Macondo Prospect (MC252) at 1522 m depth, in the east Mississippi Canyon area (N 28.73667 W 88.38694) in the northern Gulf of Mexico (NGOM), 66 km off the coast of Louisiana (LA). When the well was capped 87 days later a vast area of NGOM was oil polluted (Figure 1). According to decisions in the US v. BP trial (2015) 3.19 million barrels (roughly 500,000 m^3) of oil were released into the ocean during the spill, in addition to several hundred thousand tons of hydrocarbon (HC) gases. The response operation applied roughly 7,000 m^3 of oil-dispersing agents, 40% of it added to the gusher at the seabed and 60% to surface oil slicks offshore (but not nearshore or at the coast). The unprecedented deep-sea application of dispersant contributed to formation of large plumes of HC rich water that spread laterally in deep waters (>1000 m depth) and led to contamination of deep water habitats. Much of the oil surfaced and formed oil slicks that at their maximum on June 19 reached a size of

>40,000 km^2, and that cumulatively covered >112,000 km^2 of the ocean surface (DWH-NRDA, 2015). The spill weathering process produced oily aggregated materials which partly sank to the seabed as "marine snow". Oil slicks were pushed towards the coast by ocean currents, wind and waves and were washed onto the shoreline in LA, Mississippi (MI), Alabama (AL) and Florida (FL). More than 2100 kilometers of shoreline were affected, including beaches, marshes, wetlands and estuaries that are important habitats and nursery areas for a wide range of species. Fisheries in parts of NGOM were temporarily closed due to public concern that seafood might be contaminated with oil HCs. Research funding programs were established (see overview at: http://www.dwhprojecttracker.org/) to increase our understanding of how the DWH oil spill impacted the environment in NGOM. By January 2016 more than 500 individual research papers addressing a wide range of environmental aspects of the spill had been published in peer reviewed journals.

In this review we summarize the environmental research literature of the DWH oil spill under four key themes: (1) the environmental fate of spilled oil and gas; (2) biological/ecotoxicological effects in offshore ecosystems; (3) effects in nearshore and coastal sites; and (4) effects on long-lived marine organisms. The term *offshore* is understood as beyond the NGOM shelf edge (> 200 m depth), whereas the term *nearshore* represents the areas stretching from estuarine waters to the continental shelf edge (0 m – 200 m). Oil dispersants were not used nearshore or in connection with coastal cleanup operations during the DWH response. Nonetheless, a number of experimental studies have addressed effect issues related to dispersant application in oiled coastal systems. These studies are only superficially commented herein.

2. Environmental research on Deepwater Horizon oil spill

2.1 Fate of DWH spill

Characterization and behaviour of released oil and gas
The oil released from the MC252 well was a type A – Louisiana light sweet crude oil, which is a crude low in sulfur and high in gasoline/kerosene fractions in comparison to heavier oils. Due to the rapid pressure drop at the exit point, the oil fraction of the blowout stream was physically dispersed into small and microscopic oil droplets (10 µm – several mm). The size distribution of these oil droplets was a key factor for the fate of the oil in the subsequent seconds, minutes, days and months (Thibodeaux et al., 2011; Yapa et al., 2012; Zhao et al., 2014). As oil has a lower density than seawater, it generally moves upwards to the water surface. Large oil droplets rise more rapidly than smaller droplets; and micro-droplets smaller than a certain diameter (<70 µm) have a neutral relative buoyancy and will therefore stay entrained in the water column, unless they coalesce to form larger droplets. Small oil droplets are more prone to degradation by physical and microbial processes. Oil-dispersing chemicals break up oil into smaller

droplets and increase the stability of those droplets, thereby modulating the behaviour and the fate of the oil. The oil-dispersing agents used during DWH were mainly Corexit® 9500 and Corexit® 9527, both with dioctyl sodium sulfosuccinate (DOSS) as the main surfactant component.

Soon after the DWH explosion, large volumes of oil appeared at the surface, but because of the great depth it was suspected that an unknown but potentially large amount of the oil became trapped in deep waters (Figure 2). It was a challenge to find this deep plume and to characterize how its composition changed with time as a result of physical and microbial processes. In May 2010, Diercks et al. (2010) detected the plume at depths >1000 m by using *in situ* fluorescence and beam attenuation measurements. The plume extended mainly in a west-southwest direction from the still gushing wellhead. In the plume, they found polycyclic aromatic hydrocarbon (PAH) concentrations up to 189 µg/L (ppb) and calculated that PAH contamination at a level toxic to marine organisms extended at least 13 km from the wellhead. The depth and direction of the initial deep plume was confirmed by Camilli et al. (2010) in late June 2010. A neutrally buoyant plume was found at approximately 1100 m depth, up to 200 m high, and up to 2 km wide, extending continuously at least 35 km downstream from the wellhead. Concentrations of petroleum monoaromatics in the plume exceeded 50 µg/L and the estimated total input to the deep plume was more than twice that of natural seeps in NGOM. The latter comparison may be questioned however. Recent calculations indicate that the HC flux from natural seeps in the NGOM has been severely underestimated (Smith et al., 2014a).

A large volume of gaseous HCs were incorporated into the deep plume in addition to oil. According to Reddy et al. (2012), the blowout flow had a gas/oil ratio (GOR) of 1,600 (GOR, defined as the standard cubic feet of gas per petroleum barrel at 15.6 °C and 1 bar). In water samples collected within the deep plume with isobaric gas-tight samplers at 1100 m depth on June 21st 2010, the most abundant HCs larger than C1-C5 were benzene, toluene, ethylbenzene, and total xylenes (BTEX ≤78 µg/L) and the total amount of C1-C5 HCs released to the water column was estimated to equal 1.7×10^{11} g (170,000 tons). The plume was preferentially enriched with water-soluble components, indicating that aqueous dissolution played a major role in the deep plume formation, whereas the fates of relatively insoluble petroleum components were initially controlled by other processes. The distribution of HCs in deep waters within 45 km of the wellhead was estimated with certified HC data acquired from NOAA and BP to confirm the existence of the deep-water plume (at 1200 m depth) (Spier et al., 2013). HC contaminants were dispersed over a wider area than previously thought and dissolved benzene was found at potentially toxic concentrations outside of the areas previously reported to contain HCs. The authors suggested that an increase in less water soluble hydrocarbons in the deep waters most likely was associated with the application of dispersants at the leaking wellhead. According to Ryerson et al. (2012), the HCs in the

visible oil slicks may have represented only 15% of the total gas and oil released. Although readily-soluble HCs made up about 25% of the leaking mixture by mass, subsurface chemical data showed that these compounds made up about 69% of the deep plume mass. Only about 31% of the deep plume mass was initially transported in the form of trapped oil droplets (Ryerson et al., 2012). Petroleum HCs in surface waters of the LA continental shelf were studied by Liu et al. (2014). Concentrations of total dissolved n-alkanes (C_9–C_{35}) were more than one order of magnitude higher in May 2010 than in August 2010 and May 2011. Further, PAH concentrations in suspended particles were five times higher on average in May 2010 than in May 2011. Application of a biomarker ratio of 17α(H),21β(H)-30-norhopane over 17α(H),21β(H)-hopane confirmed that suspended particles from at least two stations were contaminated by the DWH spill in May 2010, but bulk chemical properties of the seawater, such as particulate and dissolved organic carbon (POC and DOC), were not altered by the DWH oil spill when compared against their natural variability.

Of the 7,000 m^3 of oil-dispersing agents used during the DWH response, about 40% were added at the wellhead on the ocean floor. This unprecedented procedure was controversial as it created an array of new unknowns regarding the fate and possible effects of the released oil. The US-EPA has established the aquatic life benchmark of DOSS (the main dispersant agent) to be 40 µg/L, meaning that concentrations below this reference value are not expected to harm aquatic life. Kujawinski et al. (2011) found DOSS sequestered in HC plumes at 1000-1200 m water depth. Based on analyses of water samples obtained up to 300 km away from the wellhead, and up to 64 days after dispersant applications ceased, they suggested that dilution (and not biodegradation) was the primary process affecting DOSS concentrations in the deep plume waters. Gray et al. (2014) measured concentrations of DOSS in seawater samples from various depths in NGOM during the spill. Concentrations exceeding 200 µg/L were observed in only one surface water sample near the well site where dispersant was being applied continuously. In subsurface samples, DOSS did not exceed the 40 µg/L benchmark. How the added Corexit dispersants affected the subsea-to-surface oil partitioning was investigated by Paris et al. (2012) with a coupled hydrodynamic and stochastic buoyant particle-tracking model. They suggested that the main effect of dispersants was to shift the oil plume slightly deeper, with only marginal effects on the amount of oil that surfaced. This conclusion was challenged by Adams et al. (2013), who stated that the predictions were based on unrealistically small droplet sizes for untreated oil. Aman and Paris (2013) responded and agreed that the droplet size was a significant unknown variable in the estimate of oil transport.

About 60% of the dispersants were sprayed at the surface to break up oil slicks and entrain oil into the upper part of the water column. The cumulative ocean surface over which dispersant was applied was only about 0.06 percent of the cumulative area where detectable surface oiling was observed (305 versus

475,000 square-miles/days) (DWH-NRDA, 2015). Chemically-dispersed surface oil will, depending on wave turbulence, be diluted to concentrations typically < 100 mg/L in the top 1 m of the water column. In less than 24 h, it will be further diluted to concentrations <10 mg/L in the top 10 m of the water column, before biodegradation further reduces the oil concentration to < 1 mg/L within weeks (Lee et al., 2013). Gong et al. (2014) reviewed the mechanisms by which oil, dispersed oil, and sediment particles interact. They emphasized factors controlling the fate, transport and remediation of oil spills, including sediment particle size, concentrations of oil and waterborne organic matter, oil properties, and water salinity. Key research needs were identified for data to support the evaluation of fate and impacts of oil spills and to develop effective remediation strategies, including research on sorption and desorption of oil droplets by sediment particles, and how dispersants affect these processes and the formation of aggregates of oil and suspended particulate material. The study of White et al. (2014) indicated that the DOSS component of dispersants applied to surface slicks and to subsurface oil was considerably more persistent than initially thought, when it was associated with weathered oil. They found DOSS in variable quantities in flocculent materials and surface sediments from deepwater sites 6 months after the spill and also in oily materials washed up on NGOM beaches up to several years after the spill. To assess the effectiveness of surface-applied dispersants, Bejarano et al. (2013) measured the concentrations of petroleum HCs and components of Corexit (dipropylene glycol n-butyl ether, DPnB) in seawater at 1 and 10 m depths at sites with no oil slicks, and under oil slicks before and shortly after dispersant application. Ratios of chemically-dispersed versus naturally-dispersed samples regarding sums of all PAH (total PAH; TPAH) or sums of all petroleum HCs (TPH) provided a quantitative measure of dispersant effectiveness. "Effective" and "very effective" applications displayed ratios up to 35 and 64, respectively, at 1 m depth. In two "effective" samples, TPHs and TPAHs exceeded acute toxicity benchmarks (0.81 mg/L and 8 µg/L, respectively), while none exceeded the chronic value (1,000 µg/L) for DPnB. The paper presented a tiered approach to monitoring consisting of Tier I - visual observation, Tier II - *in situ* fluorometry monitoring at 1 m depth, and Tier III - *in situ* fluorometry monitoring at 1 and 10 m depths with collection of samples for chemical analyses.

Crude oil on the sea surface spreads initially under the influence of gravity and surface tension to form slicks with an average thickness of less than 1 mm (and often as low as 0.1 mm) (Lee et al., 2013). Subsequently, the slick-thickness will either decrease or increase depending on characteristics of the oil, the influence of surface factors (wind, waves, currents, temperature, salinity, etc.) and spill response actions. *In situ* burning, widely used in the DWH response, requires thick slicks (e.g., collected by means of oil booms). About 250,000 barrels of floating oil were consumed during 411 separate burn events (DWH-NRDA, 2015). Detection of high molecular weight pyrogenic PAHs in sediment trap samples suggested that air-borne soot particles re-deposited to the Gulf surface and sank to the sea floor, together

with residues of unburned surface oil. Approximately 4% of the combusted material was released into the atmosphere as black carbon (Perring et al., 2011), and considerable amounts of polychlorinated dibenzo dioxins and furans were formed in these oil burns (Aurell and Gullett, 2010). There are few studies of the environmental impacts of the *in situ* burning, but a small number of studies addressed issues of air quality and human health, e.g., Middlebrook et al. (2012) and Jaligama et al. (2015).

The long range movement of oil slicks during the spill was primarily controlled by surface currents that depended on oceanic circulation. The dominant circulation features of NGOM include the Loop Current (LC) and clockwise running Loop Current Rings (LCRs) which are large eddies shed by the LCs, and numerous smaller cyclonic eddies that tend to form along the LC and LCR frontal boundaries. A study of Smith et al. (2014b) used *in situ* and satellite observation data to model the oceanic circulation pattern occurring in the northern and eastern gulf area during April to July 2010. A particularly large LCR was in place during this period which acted as a partial physical barrier between the NGOM and further downstream areas, such as the coast and shelf of FL. Garcia-Pineda et al. (2013) made use of Synthetic Aperture Radar (SAR) images and a Texture Classifier Neural Network Algorithm (TCNNA) for estimating oil layer thickness during the DWH spill. TCNNA outputs were used to develop an oil emulsion detection algorithm to enhance the contrast of pixels within the oil slick and to identify areas with thick, emulsified oil. Based on the good experience from the DWH spill, Caruso et al. (2013) suggested that SAR should be used more in direct spill response activities and to optimize available response resources. Several studies have used fluorescence excitation-emission matrix spectra and parallel factor analysis techniques (EEM-PARAFAC) for detecting oil degradation products in deep-water or surface-water samples from NGOM (Bianchi et al., 2014; Mendoza et al., 2013; Zhou et al., 2013a; Zhou et al., 2013b). The technique can detect oil derivatives which are transformed into the dissolved organic matter (DOM) pool, no longer recognizable as oil or oil derivatives by traditional HC analyses. In areas affected by the DWH deep plume, an oil-related fluorescence signature in the DOM pool was measureable up to 2 years after the oil spill. Maltrud et al. (2010) used ocean modeling and tracer transport simulations to investigate the possible long-term fate of the released oil. They concluded that oil-polluted waters from the DWH oil spill would be transported at relatively low (below detectable) concentrations over a significant part of the North-West Atlantic Ocean. Boufadel et al. (2014) simulated the transport and landfall of DWH oil by using satellite-observation data and NOAA models. In the period after the wellhead was capped the disappearance rate of oil from the surface was around 20% per day. The mass of oil that reached the shorelines was estimated to be 10,000 to 30,000 tons, with an expected value of 22,000 tons, or approximately 4% of the total released.

Role of HC degrading microbes in oceanic waters

Biodegradation of oil spills by marine bacteria is a complex and multistep process affected by numerous factors related to the oil itself and the environment. Marine bacteria capable of biodegradation of oil and gas HCs provided a key ecosystem service following the DWH disaster and >100 research papers have addressed this issue; for reviews, see Kimes et al. (2014), Joye et al. (2014) and King et al. (2015). Central research questions were: *How to characterize the bacterial community response?* and *Which species were most important?*

Dubinsky et al. (2013) demonstrated that multiple hydrocarbon-degrading bacteria operated simultaneously throughout the spill, but their relative importance was controlled by changes in hydrocarbon supply. For example, *Oceanospirillales*, later referred to as *Oceaniserpentilla*, and *Pseudomonas* were dominant in the early phase of the spill when n-alkanes and cycloalkanes levels were particularly high. *Colwellia*, *Cycloclasticus*, and *Pseudoalteromonas* increased in dominance later when petroleum hydrocarbons decreased and aromatic hydrocarbons increased. These microbial community shifts in the deep plume were corroborated by Kleindienst et al. (2015a). Others have suggested that the cold water proteobacteria group *Colwellia* sp. was among the most important, if not *the* most important, indigenous oil-degrading group in deep-water following the spill (Bælum et al., 2012; Mason et al., 2014a; Redmond and Valentine, 2012). The study by Mason et al. (2014a) supported the theory suggested by Dubinsky et al. (2013), that the dominating non-gaseous, n-alkanes and cycloalkanes in the early phase were degraded mainly by *Oceanospirillales*, whereas the gaseous, simple aromatic HCs dominating in later phases were degraded mainly by *Colwellia*. As well, gamma-proteobacteria closely related to known petroleum degraders bloomed in the cold waters of the deep plume, leading to increased HC biodegradation rates and a half-life of oil in the range of 1.2-6.1 days (Hazen et al., 2010).

According to Valentine et al. (2010) volatile HC gases, such as propane and ethane, were key drivers of the microbial response and HC respiration in the deep plumes. They suggested that propane and ethane trapped in deep waters may have accounted for up to 70% of the observed oxygen consumption in the fresh plumes, and that respiration by low-diversity bacterial communities 'primed' the HC-degrading bacterial populations in aging plumes. Although the gas-rich deep-water plumes were a short-lived feature, methane concentrations in the water column remained above background in NGOM waters throughout 2010. Microbial methane oxidation in the deep-water plumes peaked with record high rates, 5,900 nmol/L per day, in May and early June 2010, coincident with a rapid rise in the abundance of methane-oxidizing microbes (Crespo-Medina et al., 2014). Subsequently, in late June, the methane oxidation rate fell to < 50 nmol/L per day, despite the persistence of methane in the water column, and it continued to decline during the rest of the year. The authors suggest the precipitous drop in methane

degradation in June was a caused by depletion of essential nutrients limiting the activity of the methane-oxidizing bacteria.

Biodegradation processes also included degradation of transformation byproducts and exopolymeric substances that were produced by microbes to emulsify HCs and facilitate access to the oil. Ziervogel and Arnosti (2014) measured enzymatic hydrolysis of carbohydrates and peptides in water samples obtained from within and outside of the deep plume (6 stations 0.9-17.3 km from the well, 900-1240 m depth, May 30-June 05, 2010). They proposed that exopolymeric substances and other transformation byproducts in the deep-water plume may have enhanced heterotrophic bacterial metabolism. A higher peptidase activity and enzymatic hydrolysis of carbohydrates inside compared to outside the oil spill plume indicated that microbial communities associated with the deep-water plume were primed to degrade a selected range of specific high molecular weight substrates. Gutierrez et al. (2013) investigated the role of amphiphilic exopolysaccharides produced by indigenous *Halomonas* bacteria in the fate of the DWH oil. Microbial samples were collected from oil-contaminated surface waters during the active spill phase. *Halomonas* exopolysaccharides produced by strain TG39 effectively increased the solubilization of aromatic HCs and enhanced their biodegradation, thus contributing to the removal of the oil and to the formation of oil aggregates. The data provided unequivocal evidence of the HC-degrading qualities of some of the dominant taxa enriched in surface and plume waters during the DWH oil spill, and a more complete understanding of their role in the fate of spilled oil.

Nutrient shortage is a normal limiting factor for microbial growth. Edwards et al. (2011) suggested that microbial growth in oil-contaminated surface waters of the NGOM was limited by a shortage of dissolved nutrients, in particular phosphate, because bacterial cell numbers and biomass increased rapidly when incubation mixtures were amended with nutrients. Atlas & Hazen (2011) highlighted the benefit of adding fertilizers containing nitrogen to stimulate oil biodegradation, especially on shorelines. Similarly, a review by Ron and Rosenberg (2014) identified nitrogen and phosphorous as the main rate-limiting factors for oil degradation in the sea. They suggested using uric acid as a fertilizer for enhancing oil bioremediation at sea because it is the major nitrogen waste product of many animal species, has low solubility in water, and adheres to hydrocarbons. Nutrient depletion may also be a proxy for growth of oil-degrading microbes. Shiller and Joung (2012) correlated nitrate, phosphate and oxygen depletion in the DWH deep plume. A substantial portion of HCs in the deep plume was converted to biomass (0.8 - 2 x 10^{10} mol C), whereas in surface waters the growth of oil degraders was nutrient-limited. This indicates a need to monitor changes in nutrients and nutrient recycling in future spills.

Oxygen depletion and the development of large anoxic dead zones within NGOM due to the microbial degradation of hydrocarbons were considered as a possible scenario in the early phase of the DWH spill.

Fortunately, this worst-case scenario of total anoxia did not occur although several studies demonstrated that HC biodegradation consumed massive amounts of oxygen and caused a persistent oxygen anomaly in deep gulf waters, e.g., (Dubinsky et al., 2013; Kessler et al., 2011; Valentine et al., 2010). According to Kessler et al. (2011) an estimated 3.0 - 3.9 x 10^{10} moles of oxygen were respired in deep waters, primarily by methanotrophic bacteria during 120 days following the onset of the spill. Most of the released methane was removed, but a persistent oxygen anomaly remained along with a residual microbial community dominated by methanotrophs. However, Joye et al. (2011) disagreed, stating that there was too much uncertainty in the work to support this conclusion.

Formation of oil-rich aggregates, or flocs, is an important fate of spilled oil, involving complex interactions among bacteria, phytoplankton, and zooplankton. The flocculent materials may stay suspended within the surface water or precipitate to the seabed as marine oil 'snow'. Arnosti et al. (2014) demonstrated that laboratory-generated oil aggregates were hotspots for a complex microbial petroleum degradation activity. An intense formation of aggregates was observed in the upper water column early in the DWH spill as the precursors to a massive pulse of oil-derived materials that settled to the sediments near the wellhead in the weeks following the accident. This substantial sedimentation of marine snow and the subsequent enhanced respiration of organic carbon, caused reducing conditions in the upper sediment layers over a large area of NGOM, as indicated by changes in redox sensitive metals (Mn, Re and Cd) (Hastings et al., 2014). To characterize the marine snow formation process Passow et al. (2012) conducted roller table experiments with plume water. They found that oil-rich marine snow was formed through a complex interaction of three mechanisms: (1) production of mucous webs through activities of bacterial oil-degraders associated with floating oil; (2) production of oily particulate matter through coagulation of oil with suspended matter; and (3) coagulation of phytoplankton with oil droplets incorporated into aggregates. Ziervogel et al. (2012) found that microbial activities and dissolved organic matter dynamics in oil-contaminated seawater were greatly affected by activities of microbes associated with macroscopic oil aggregates. The aggregates mediated transfer of HCs from the surface to the deep sea by two distinct mechanisms, (a) a microbially-driven flux of oil-derived DOC from sinking oil aggregates, and (b) a rapid sedimentation of the oil aggregates themselves, which were vehicles that transported oily particulate matter and oil aggregate-associated microbial communities. A subsequent study by Ziervogel et al. (2014b) found only a moderate stimulation of microbial metabolic rates in sediments affected by the oil-aggregate fallout during DWH, and no consistent increase of microbial activities and secondary biomass production. In contrast, Mason et al. (2014b) demonstrated that indigenous bacteria in deep-water sediments contributed significantly to degradation of linear alkanes and simple aromatics in the fallout, but that PAHs were persistent.

Cold seeps that leak oil or gas are common in NGOM, and research studies have shown that seawater from areas with much seepage activity has an increased abundance of indigenous oil degrading bacteria, e.g., (Hazen et al., 2010; Smith et al., 2014a). Ziervogel et al. (2014a) sampled surface water from the Green Canyon area for a roller tank experiment to test whether oil slick residues originating from natural oil and gas seeps facilitated the formation of marine snow. Samples with natural background oil contamination displayed a temporal shift of microbial cycling of organic matter which possibly affects food web interactions and carbon cycling in such areas. Rivers et al. (2013) measured microbial community responses in water samples collected at two stations 6-8 km downcurrent of the DWH well in late May/early June 2010, both inside and below the deepwater plume. The response was profoundly influenced by petroleum contamination, even in samples where the plume signals were non-detectable with *in situ* instrumentation. The authors pointed to the influence of natural seeps in the area to explain the observed response, as some of the bloom-forming taxa were present even one month before the DWH accident. Hawley et al. (2013) investigated natural oil-degrading bacteria communities present in crude oil samples collected from natural seeps in the Santa Barbara Channel offshore Southern California. The dominant bacteria were primarily from chemolithoautotrophic bacteria classes, in contrast to the oil degrading bacteria blooming in the DWH oil spill plume which were dominated by *Oceanospirillales*, a bacterial order belonging to the Deltaproteobacteria. This difference might be explained by anoxic conditions at the SBC oil seep, while the DWH oil plume was oxic. Also Mason et al. (2012) investigated the functional role of *Oceanospirillales* bacteria and other active members of the indigenous microbial community in the DWH deep plume, using deep sequencing of bacterial community DNA and RNA, as well as single-cell genomics. Genes for motility, chemotaxis and aliphatic HC degradation were significantly enriched and expressed in the HC plume samples compared to samples of uncontaminated seawater at the same depth. The data indicate a rapid response of *Oceanospirillales* to aliphatic HCs in the deep sea plume in the early phase of the oil spill.

Oceanic mixing and circulation processes in NGOM were important cofactors to the microbial oil-degradation. Valentine et al. (2012) used a new coupled physical-metabolic model to assess the effect of physical mixing processes on marine bacterial communities and their capacity for HC degradation and oxygen consumption. Biodegradation patterns were well-described by exponential growth of bacteria from seed populations naturally present at low abundance. It is likely that oceanic mixing processes played a key role in distributing HCs and associated bacterial blooms within the northeast Gulf waters. The oceanic mixing processes also accelerated HC degradation through an autoinoculation effect. As a consequence, HC-degrading bacteria persisted at a higher abundance in waters that previously had been blooming and that later re-circulated to the spill site, feeding successive bacterial blooms, highlighting the effects of

mixing and circulation processes on biodegradation of oil during spills and suggesting an important role for mixing in the microbial ecology of deep ocean environments.

How did the application of dispersants modulate the response of oil degrading microbes in deep water and surface water? This problem has been studied most frequently with laboratory mesocosms. According to Chakraborty et al. (2012) added dispersants were not toxic to indigenous oceanic microbes at the concentrations used, and different bacterial species isolated in the aftermath of the spill were able to degrade the HCs as well as glycols and DOSS components of the Corexit dispersant. Du and Kessler (2012) found that HC consumption rates were positive correlated with the addition of dispersants at the wellhead. The peak in HC respiration occurred around mid-July 2010 when dispersant use was most intense, indicating that the addition of dispersants at the wellhead contributed to make conditions (small oil droplets) that accelerated HC respiration. Also Prince et al. (2013) reported that Corexit dispersants accelerated the biodegradation of a lightly weathered Alaska North Slope crude oil, reducing the HC half-life in the degradation setup from 13.8 to 11 days. Brakstad et al. (2014) found that biodegradation of n-alkanes was significantly faster in chemically-dispersed MC252 oil than in physically-dispersed oil; no such effect was observed for 3- and 4-ring PAHs. They also measured higher cell densities of oil-degrading bacteria in the chemically-dispersed mixtures. The biodegradability of dispersant (Corexit 9500) and dispersed oil differed between bacteria cultures isolated from deep/cold water and from warm water (Campo et al., 2013). Warm-water bacteria rapidly and completely degraded DOSS, alkanes, and aromatics, whereas the cold water culture metabolized the same compounds only after a lag of 28 d and with residuals consisting of iso-alkanes, n-C30-35, and 4-ring PAHs. In a microcosm study, Kleindienst et al. (2015b) found suppressive effects of dispersants on certain deepwater oil biodegraders (*Marinobacter*), but that study was recently challenged by Lewis (2015) for using dispersant concentrations approximately 2,500-4,500 times higher than the maximum measured in the plume at the DWH incident.

Role of sunlight on fate of surface oil

Photochemical degradation of oil constituents, such as PAHs, in thin surface films exposed to sunlight represents an important fate process for marine oil spills. Sunlight irradiation of weathered oil mixtures degrades large, aromatic HC molecules and generates oxidized species that are more water soluble than the parent compounds. The studies by Ray et al. (2014) and Radović et al. (2014) investigated the complex formation of oxygenated transformation products when WAFs of oil are exposed to sunlight. Ray & Tarr (2014) further studied the key role of hydroxyl radical production in the oil photodegradation process and how the adding of TiO_2 photocatalysts can speed up oil degradation. Oil photodegradation and its enhancement by TiO_2 photocatalysts was also investigated by Brame et al. (2013) who used food-grade TiO_2 to accelerate HC degradation in the laboratory. Similarly, King et al. (2014) found that PAHs were

readily photodegraded whereas larger *n*-alkanes were generally resistant to photodegradation. Sunlight irradiation of oil in surface thin films facilitated biodegradation of weathered mixtures but also increased the toxicity of seawater in contact with the oil, as measured by the Microtox™ test, presumably due to the increased release of toxic, water-soluble photoproducts of the PAH (King et al., 2014). In contrast, DOSS was resistant to direct photolysis by normal sunlight alone, but that presence of hydroxyl radicals in seawater significantly increased UV based hydrolysis and degradation of DOSS, apparently by photosensitization (Batchu et al., 2014; Glover et al., 2014).

Chemical fingerprinting of DWH oil spill

Chemical fingerprinting uses the chemical signatures of a crude oil or its degradation products to track the origin of a spill. With time, spilled oil is modified by weathering processes such as evaporation, dissolution, biodegradation and photo-oxidation, leading to a decreased proportion of labile constituents and an increased proportion of recalcitrant substances in the residual oil. Diverse chemical classes that are commonly found in petroleum mixtures but that vary considerably in their relative concentrations among different oils may be used for fingerprinting; such as hopanoids, tricyclic or tetracyclic steranes, long-chain alkylbenzenes and alkyltoluenes. Mulabagal et al. (2013) used GC/MS methods for fingerprinting hopanes and steranes in weathered tar balls collected from AL's beaches during June 2010 to 2012. A characteristic pattern of hopane and steranes linked all these tar balls to the DWH oil spill. Aeppli et al. (2012) and White et al. (2012a) used comprehensive two-dimensional GC analyses (GC×GC-FID and GC×GC-MS) for chemical fingerprinting of various sample materials as these techniques provide improved resolution and quantification and therefore better fingerprinting of oil-derived chemical signatures. Valentine et al. (2014) studied publicly available data of 17α(H),21β(H)-hopane (i.e., C-30-hopane), a conservative marker of oil contamination, in sediments collected from more than 500 different locations in NGOM. Over a wide area, sediments at great depths were indeed oil-contaminated, and the distribution of C-30 hopane was consistent with DWH spill as the source. They described the contamination footprint as a massive "bathtub ring" which was formed by oil-rich water in the deep plume at 900–1,300 m depth impinging laterally upon the continental slope and by a "fallout plume" of suspended oil particles sinking to the seafloor at depths of 1,300–1,700 m.

Aeppli et al. (2014) analyzed hopanoids, steranes, and triaromatic steroids in oiled seawater and in shoreline samples that had been subjected to different degrees of weathering for up to 28 months after the spill. Hopanoids with up to 31 carbons, steranes and diasteranes were the most persistent fingerprinting markers that revealed the DWH spill as the source. In coastal samples, Hall et al. (2013) characterized the oxygenated hydrocarbons (OxHCs) formed during the weathering of Macondo oil. These heavily weathered products likely originated from saturated HCs and not from aromatic HCs, and represented an

underreported class of persistent oil spill contaminants. Liu et al. (2012) compared the chemical profiles of petroleum HCs and elements detected in sediments close to the Macondo wellhead and in samples of oil mousse collected from the sea surface and from salt marshes oiled by the DWH spill. The patterns found in the different sample matrices were consistent with the projected movement of oil from the accident site to coastal salt marshes. Oil deposited in sediments was only lightly to moderately degraded one year after the spill. In sediments downstream of the well there was a statistically significant increase in Ni, Cr, and Pb concentrations three months after the oil spill, but one year later, concentrations had decreased significantly, close to pre-spill conditions (Steffy et al., 2013). The study indicated that differences in Ni concentrations and V–Ni ratios were effective means for monitoring contamination from the spill.

2.2 Contamination and effects of the DWH spill on offshore organisms and ecosystems

Uptake and effects in oceanic microbiota and plankton
Oil exposure conditions in the field are often simulated in the laboratory by subjecting test organisms to specific concentrations of a water accommodated fraction (WAF) of petroleum mixtures for specific time periods. A WAF can be defined as a dispersed and diluted mixture of the oil in seawater without visible floating or droplet oil. WAFs can be created by high energy mixing (i.e. high-energy WAFs, HEWAFs, physically or mechanically dispersed oil), or by adding oil-dispersing agents to the oil during mixing with water (i.e. chemically-enhanced WAFs, CEWAFs, chemically-dispersed oil). The possibility that contaminants from the DWH spill could accumulate in marine food webs and seafood led to periodic closures of commercial fishing areas, sometimes comprising more than 30% of the total in the NGOM. Web-based tools for assessing the economic impacts of the DWH spill on fish resources demonstrated that a significant profit loss in NGOM fisheries was caused by the closures (Chakrabarty et al., 2012; Sumaila et al., 2012). There was early evidence that oil-derived carbon indeed entered the planktonic sections of the marine food web (Graham et al., 2010). Near Mobile Bay, AL, a depletion of the stable carbon isotope $\delta^{13}C$ in two size classes of plankton coincided with the arrival of surface oil slicks in the area. The stable carbon isotope $\delta^{13}C$ was depleted in petroleum HCs in comparison to recent photosynthetically-derived carbon, a finding corroborated by Chanton et al. (2012). The ratio between $\delta^{13}C$ and the unstable isotope $\Delta^{14}C$ in plankton mixtures and in dissolved inorganic carbon (DIC) of water samples decreased within 100 km of the spill site and in surface water from coastal and offshore sites. $\Delta^{14}C$ was depleted in plankton relative to DIC in the region down-current of the spill site, and there was a significant linear correlation between $\Delta^{14}C$ and $\delta^{13}C$ in plankton samples. Both findings were consistent with the hypothesis that carbon released from the DWH spill contributed to the offshore planktonic food web, and Chanton et al. inferred that the methane component of the spill was an especially important source of petrogenic carbon. Petrogenic carbon possibly entered the marine planktonic food web through small particles indicative of

methanotrophy (Cherrier et al., 2014), while PAHs from the DWH spill entered the NGOM food web via planktonic meso-zooplankton (Mitra et al., 2012).

Chemical dispersion of surface oil during the spill led to questions of how plankton (bacteria, phytoplankton, zooplankton) would respond to dispersed oil in comparison to undispersed oil. Tests with three microbial bioassays demonstrated that genotoxic and mutagenic effects of contaminants from the DWH oil spill were traceable in seawater and sediments, even far downstream in the NGOM and for at least 1.5 years after the blowout (Paul et al., 2013). However, Prince and Parkerton (2014) claimed that these conclusions were not supported by objective data, and that the study provided little evidence of toxicity gradients or a realistic underlying causality. For an alternative weathered oil, Alaska North Slope crude, environmentally-realistic concentrations of CEWAF dispersed with Corexit 9500A were toxic to the ammonia-oxidizing bacterium *Nitrosomonas europaea*, whereas dispersant-alone and WAF-alone were not toxic (Radniecki et al., 2013). Ortmann et al. (2012) showed that chemical dispersant or CEWAF added to mesocosms increased the biomass of heterotrophic prokaryotes and inhibited ciliates indicating that dispersion of DWH oil may have caused a reduction in transfer of carbon by grazers to higher trophic levels on the AL shelf. Autotrophs were also sensitive to dispersants. Chemical dispersion of two oils with different degrees of weathering (fresh crude and tar mat oil) increased growth inhibition of phytoplankton in lab tests (Garr et al., 2014). Judson et al. (2010) compared the toxicity and endocrine effect of eight different oil dispersants. Bioassays with mammalian cells in culture showed that most dispersants (6 of 8) were of equivalent cytotoxicity (median LC50s about 100 mg/L) whereas two were about 10 times less cytotoxic. No androgenicity was found, although two of eight dispersants showed faint signs of estrogenicity; neither were Corexit. It should be noted that dispersants during DWH response operations were only applied offshore and not in coastal or nearshore operations.

DWH oil may have also affected phytoplankton at the community level. Hu et al. (2011) combined satellite measurements with numerical circulation models and other environmental data to assess phytoplankton production. A chlorophyll a anomaly was observed within an area exceeding 11,000 km^2 in the north-east GOM during August 2010 (3 weeks after well capping), although the estimate is considered as uncertain. Gilde and Pinckey (2012) used *in situ* microcosms exposed to crude oils to demonstrate that low oil concentrations could reduce biomass production and alter phytoplankton community composition with possible cascading effects. Similarly, three different microcosm experiments demonstrated that dispersant significantly increased the toxicity of crude oil to phytoplankton communities (Ozhan and Bargu, 2014). Ten-day exposures decreased the abundance of sensitive species and increased the abundance of more resistant species, particularly under nutrient-limited conditions, highlighting the

possibility that different nutrient regimes play a major role in determining shifts in phytoplankton community structure in response to crude oil and dispersant exposure.

Faksness et al. (2015) prepared WAFs of Macondo source and field-collected oil and tested their toxicity to the algae *Skeletonema costatum* and the herbivorous copepod *Acartia tonsa*. The source oils contained a large fraction of soluble and bioavailable components such as BTEX and naphthalene, whereas these components were depleted in surface-collected oils. The acute toxicity expressed as percent lethality (*A. tonsa*) and growth inhibition (*S. costatum*) in undiluted WAF decreased with an increasing degree of weathering, and the copepods were more sensitive to water soluble HC than the algae. Effect assessments in marine micro- and meso-zooplankton are particularly important for understanding higher-level ecosystem impacts of oil spills. The mini-review of Abbriano et al. (2011) discussed this issue based on a few of the earliest studies of effects on plankton after the DWH spill. Carassou et al. (2014) studied mesozooplankton data from a long-term plankton survey off the coast of AL, and found evidence of a significant but short-term impact of the oil on zooplankton assemblages. While some taxa decreased in density, others increased. An increased production of zooplankton in response to oil stimulation of microbial activity, or the removal of the top-down control caused by fishing closures, may have initiated a cascade of indirect effects. In a series of articles, Almeda and others addressed the effects of DWH WAF and CEWAF on different size classes of oceanic zooplankton, including microzooplankton (Almeda et al., 2014b), mesozooplankton (Almeda et al., 2013b), copepods (Almeda et al., 2014a; Cohen et al., 2014), and large gelatinous zooplankton species (Almeda et al., 2013a). Small ciliates and copepods were particularly sensitive. For copepods, exposure to crude oil alone reduced egg production rates, fecal pellet production rates, and egg hatching, but CEWAF was more toxic than WAF. Studies with larger gelatinous zooplankton such as scyphozoans and ctenophores indicated that some of these much larger species were sensitive to bioaccumulation and effects (Almeda et al., 2013a). Gelatinous zooplankton may act as vehicles for contaminant transfer up the food web to apex predators such as turtles. There is still insufficient evidence of the extent to which oil was transferred to the next trophic level, and how dispersants influenced the degree of impacts on zooplankton under field conditions.

By using mesocosm experiments and aerial surveys, Powers et al. (2013) examined the effects of DWH oil on *Sargassum* brown algae communities in the pelagic zone ("pelagic": neither close to the bottom nor near the shore). Floating *Sargassum* provides a key oceanic habitat and supports a diverse assemblage of marine turtles, fish and invertebrates. Following dispersant-only and CEWAF treatments, they observed that *Sargassum* sank from the surface within 24–48 hours of treatment, suggesting that dispersed oil affects the *Sargassum* buoyancy. In contrast, *Sargassum* exposed to oil-only did not sink for most of the

experiment. Aerial surveys in 2010, 2011, and 2012 indicated oil exposure of *Sargassum* mats, but interpretation of these observations was hampered by a lack of pre-spill baseline data.

Deep sea benthos and corals

A large fraction of the DWH oil reached the seafloor via a massive sedimentation-pulse of oil aggregates (oil snow) that continued until late summer 2010 (Passow et al., 2012; Ziervogel et al., 2014b). This 'dirty blizzard' posed a risk for benthic fauna. Chanton et al. (2014) used an inverse isotopic approach to estimate the amount of oil that actually reached the seabed. Radiocarbon measurements of surface sediments in a 2.4×10^{10} m^2 deep-water region surrounding the well indicated deposition of 1.6 to 2.6×10^{10} grams of oil-derived carbon (1.6 to 2.6 g/ m^2). This quantity approximated 0.5-9.1% of the released petroleum HCs, with a best estimate of 3.0−4.9%, although the authors noted that this estimate was probably conservative. Similar estimates using hopane as a tracer were 1.8 to 14.4% of the total oil deposited in the seabed (Valentine et al., 2014).

Impacts of oil snow were investigated in different categories of benthic communities inhabiting soft bottom sediments in the vicinity of the DWH well, included meio- and macrofauna (Landers et al., 2014; Montagna et al., 2013; Wei et al., 2012), megafauna (Felder et al., 2014; Valentine and Benfield, 2013), seaweeds (Felder et al., 2014) and deep-water corals (Fisher et al., 2014a; Fisher et al., 2014b; Hsing et al., 2013; Prouty et al., 2014; White et al., 2012a). The sedimentation pulse of organic-rich material changed sediment redox conditions, with a subsequent change in profiles of the redox-sensitive metals manganese, rhenium and cadmium (Hastings et al., 2014). The density of benthic foraminifera decreased at the same depth intervals as changes in reducing conditions, suggesting that changes in redox had consequences for biota. Schwing et al. (2015) reported elevated PAH concentrations associated with freshly-deposited flocculent material and a large die-off (80-93% density reduction) of benthic foraminifera northeast of the wellhead on the continental slope. Persistent reducing conditions (up to 10 months after the event) in the sediment surface were suggested as a possible cause of the decline.

Diversity indices of soft sediment fauna are widely used to indicate environmental quality at offshore oil fields. Wei et al. (2012) constructed a composite database from six surveys between 1983 and 2003 and mapped the distribution of macrofaunal biomass in the deep NGOM. The database included stock assessments and biomass predictions from 669 sediment cores obtained from 170 locations and provided an important pre-spill baseline. From Sept. to Oct. 2010, Montagna et al. (2013) examined deep-sea benthic macro- and meiofauna communities at 68 stations at variable distances from the blowout site and found a severe reduction of faunal relative abundance and diversity extending 3 km from the wellhead in all directions, covering an area of about 24 km^2. Moderate impacts occurred up to 17 km to the southwest and 8.5 km to the northeast of the wellhead, comprising an area of 148 km^2. The effects were correlated to

concentrations of TPH, PAHs, and barium in sediments and distance from the wellhead, but not to the distance from natural HC seeps in the area. Given the deep-sea conditions, the authors suggested that recovery of the deep-sea soft-bottom habitat and the associated communities may take decades or longer. In contrast in 2012, there were no significant correlations between meiofauna densities and sediment concentrations of metals and PAH at five more shallow stations at the shelf edge that may have been affected by marine snow fallout from the DWH oil spill (Landers et al., 2014). There was also a positive microbial response to petroleum enrichment indicated by increased species richness of ciliated protists in the nepheloid layer and water column at deepwater sites affected by the spill (Moss et al., 2015). Valentine and Benfield (2013) used ROV data to compare benthic communities before and after the DWH spill at five study sites within the Mississippi Canyon lease area (an area larger than Mississippi Canyon itself). Among the study sites, there were clear differences in the taxonomic composition and abundance of benthic megafauna, benthic boundary layer plankton, and fishes. Taxonomic richness and abundances were generally lower at the site located to the south, consistent with the reported trajectory of the deep plume, which the authors attributed to mortality, emigration, or some unmeasured factor. Similarly, the overall lower abundance and diversity at the 500-N site suggested that HC concentrations were sufficiently high within 500 m of the well to induce mortality, emigration, or both. The widespread presence of carcasses of colonial and pelagic tunicates suggested that the spill affected invertebrate assemblages within at least a 2000 m radius of the blowout, and that certain taxa were more resistant; while others, e.g., sea pens and glass sponges, were more sensitive.

Felder et al. (2014) measured the abundance of seaweeds and decapod crustaceans associated with rhodoliths on shallow offshore banks in the northwestern GoM after the spill. Six cruises conducted from Dec 2010 to Oct 2013 at Ewing and Sackett Banks (55-75 m depth) revealed a decline of seaweeds and a reduction of decapod crustacean abundance and diversity. The decline of decapods largely reflected the loss of seaweed cover, and a potential cascading effect on direct consumers and animals at higher trophic levels. However, the Banks were too shallow and too distant (115-270 km) from the Macondo site to make the effects plausible.

Colonies of deep-water (or cold-water) corals represent key benthic habitats in the deep ocean (Demopoulos et al., 2014) and long-living deep-water corals may be used as sentinel species that provide a lasting visible record of deleterious impacts that cannot be detected for most deep-living mobile species (Fisher et al., 2014a). For example, patchy covering of hydrozoans on dead parts of corals can be used as a marker of damaged colonies. The health status of seven known deep-water coral sites within a 25 km radius of the Macondo wellhead has been monitored since 2010. Corals at four sites located to the south, southwest, southeast, and east of the wellhead showed some degree of injury coincident in time with the

DWH spill. Corals initially covered by floc containing DWH oil and dispersant subsequently died or sloughed off tissue. Branch loss is still occurring and injured coral branches have been colonized by opportunistic hydroids (Fisher et al., 2015; Fisher et al., 2014b; White et al., 2012a, b; White et al., 2014). At a site 11 km southwest of the wellhead, corals were covered by a brown flocculent material containing hopanoid markers consistent with the DWH oil spill as the source. The corals displayed varying degrees of stress, such as tissue loss, sclerite enlargement, excess mucous production and bleached commensal ophiuroids (Hsing et al., 2013; White et al., 2012a). At one site located 6 km south of the Macondo wellhead, >90% of the corals showed sign of injury (Fisher et al., 2014b). Another coral community, 22 km southeast of the wellhead at 1,850 to 1,950 m depth was also affected, though to a smaller degree; this discovery extended the distance and depth range of the possible impact zone considerably. The possible coral impact zone was also expanded by a HC signal in the particulate organic carbon pool of corals at nearly all sites within 30 km of the DWH spill site (Prouty et al., 2014). In an experimental setup, DeLeo et al. (2015) examined the acute toxicity of oil, WAFs, dispersant, and CEWAFs to three deepwater corals, *Paramuricea* type B3, *Callogorgia delta* and *Leiopathes glaberrim*, living at depths between 500 and 1100 m near the DWH spill site. Treatments including dispersants (dispersant alone and oil-dispersant mixture) were significantly more toxic than oil alone. As deep-water corals are extremely long-lived, the death of a colony or a whole coral field represents an irreversible and serious ecological impact. Fortunately, most known deep-water coral communities in the NGOM were not apparently injured by the spill.

Pelagic fish

Following the DWH blowout, there were no documented cases of fish-kills in offshore waters, possibly because adult fish could have avoided very contaminated waters, and surface oil was patchy. Many fisheries in NGOM were closed intermittently because of the increased potential for oil contamination of pelagic seafood species. To complement human sensory panels (e.g., Ylitalo et al. (2012)), seafood safety was also monitored by chemical screening (Bencsath et al., 2015; Genualdi et al., 2013; Gratz et al., 2011). The systematic monitoring in oil affected offshore regions found little evidence for fish seafood being significantly contaminated (Ylitalo et al., 2012). In areas less affected by the spill, fishermen-led testing of fish fillets (muscle) of seven different reef species demonstrated no notable concentrations of PAHs, selected metals, or constituents of dispersant that could be clearly linked to the spill (Fitzgerald and Gohlke, 2014). PAHs were detected in just 2 of 92 samples, and the isomer profiles suggested pyrogenic rather than petrogenic contamination. While analyzing fish fillets is needed to assess seafood safety, hydrocarbon concentrations in muscle (or even liver) are less sensitive markers of oil contamination than PAH metabolites in bile of the same fish (Beyer et al., 2010). For example, concentrations up to 470,000 ng naphthalene equivalents/g bile wet weight were measured in red snapper (*Lutjanus campechanus*)

collected in 2011 along the continental shelf edge north of the Deepwater Horizon site (Murawski et al., 2014). The array of parent PAHs and alkylated homologs in livers was correlated to the composition of DWH oil, but not to other sources of PAH in NGOM. Concentrations of biliary PAH metabolites also declined between 2011 and 2012, consistent with a second large survey of biliary PAH metabolites in red snapper between 2011 and 2013 (Snyder et al., 2015). The spatial distribution of metabolites suggested the DWH spill as a source, with higher concentrations closer to the spill. However, metabolites as chemical markers of oil exposure were inconsistent among species surveyed and the metabolites measured. The bile of Golden tilefish (*Lopholatilus chamaeleonticeps*) contained very high concentrations of naphthalene metabolites, but spatial and temporal distributions were unrelated to the DWH spill, possibly because tilefish consume sediment when feeding. Unlike naphthalenes, the concentrations of BaP metabolites in all species tested were not related spatially or temporally to the spill, indicating that chemical markers of exposure must be validated before use.

Concern for oil effects on early life stages of fish arose from laboratory studies of developmental cardiotoxicity in response to the Exxon Valdez oil spill (EVOS) (Incardona et al., 2013). Comparisons of the toxicity of Alaska North Slope crude oil (ANSCO; EVOS) and MC252 (DWH spill) to early life stages of zebrafish (*Danio rerio*), a well-studied model of oil embryo toxicity, demonstrated that effects of MC252 crude oil were consistent with injuries caused by ANSCO. Cardiac and cranio-facial deformities and tissue distribution of cytochrome P4501A (CYP1A) induction, an indicator of PAH exposure, were largely indistinguishable between MC252 and ANSCO-exposed larvae and generally correlated with the PAH composition of each oil. This research linked the established literature on oil toxicity to fish embryos to the assessment of natural resource injury for marine species and was subsequently extended to native species of NGOM. The cardiotoxicity of Macondo oil to embryos of commercially- and ecologically-important predatory fish (bluefin tuna *Thunnus thynnus;* yellowfin tuna *T. albacares;* amberjack, *Seriola, spp.*) was evident at 1–15 µg/L of TPAH in exposure solutions, irrespective of oil weathering (Incardona et al., 2014). The mechanism of cardiotoxicity was established with isolated cardiomyocyte cells from juvenile bluefin and yellowfin tuna. In cells exposed to oil, membrane signal transduction was disrupted by interference with the regulation of potassium and calcium ions (Brette et al., 2014). Impaired signaling and coordination of cardiac contractions may cause arrhythmias and could explain the impaired swimming performance of juvenile mahi-mahi (*Coryphaena hippurus* or common dolphinfish). There was a 4.5-fold increase in the prevalence of pericardial and yolk sac edema in larvae exposed briefly (48 h) to low concentrations of oil (e.g., 1 µg/L TPAH), and in juveniles that had survived exposure without signs of cardiotoxicity, swimming performance was impaired relative to unexposed fish (Mager et al., 2014). In mahi-mahi exposed to MC252 oil, cardiotoxicity was also associated with the down-regulation of genes related to myofiber structure and contractility, and up-regulation of *cyp1a* (Edmunds et al., 2015). The

acute lethality and sublethal cardiotoxicity of weathered MC252 oil was about 3- to 5-fold greater than that of un-weathered oil, likely because the highly toxic 3-ringed PAH were more concentrated in weathered oil (Esbaugh et al., 2016). Impaired swimming performance corresponded to a higher routine energy demand of chub mackerel (*Scomber japonicas*) measured by swim tunnel respirometry after a 96 h exposure to WAF of weathered MC252 oil (Klinger et al., 2015). Overall, embryo toxicity followed by lower swimming ability and aerobic capacity of juveniles suggest a high risk for reduced productivity of commercially-important pelagic fish species exposed to DWH oil. However, effects depend entirely on the extent of exposure. Satellite imagery of oil distribution and models of the spawning habitats of bluefin tuna indicated that some eggs and larvae were present in oil-contaminated waters in the eastern part of NGOM (Muhling et al., 2012). The highest densities of larvae were in the western Gulf, so that <10% of spawning grounds and <12% of the larvae were exposed to oil-contaminated water. Similarly, the distribution of larvae of blackfin tuna (*T. atlanticus*), blue marlin (*Makaira nigricans*), mahi-mahi, and sailfish (*Istiophorus platypterus*) in the NGOM overlapped somewhat with the distribution of surface oil. While larval abundance in 2010 following the spill appeared lower compared to the preceding three years, their distribution and abundance could not be clearly linked to the spill because of the dominant influence of other oceanic conditions (Rooker et al., 2013). There is a need for more research on field experiments and new sampling strategies to test potential links between exposure of early life stages of fish to oil, prevalence of cardiotoxicity, impairment of swimming capacity, and changes in population rates of growth and productivity. This and other effect issues in fish are also discussed in the costal fish section.

2.3 Contamination and effects in nearshore and coastline habitats and organisms

Fate of stranded oil

Although only a minor portion of the DWH oil reached the shoreline, the amount was enough to cause widespread contamination of coastal habitats and ecosystems, including many salt marshes, wetlands and estuaries. Landfall of oil is generally considered an unfavorable situation in comparison to oil remaining at sea, because stranding causes a multitude of new environmental impacts and worsens the impacts on fisheries, tourism, and other societal sectors. Variable figures exist on the total length of coastline that was affected by the DWH oil spill. According to the draft DWH NRDA report, oil stranding affected at least 2,100 kilometers of coastline in the states of LA, MI, AL, FL, and TX, including beaches (51 percent of affected coastline), marshes (45 percent), and other (mostly) manmade shorelines (4 percent) (DWH-NRDA, 2015). According to Michel et al. (2013), various degrees of oiling were documented on 1773 km of shoreline, whereas cleanup activities, managed under the Shoreline Cleanup Assessment Technique (SCAT) Program, were authorized on 660 km of shoreline, or 73.3% of oiled beaches and up to 71 km, or 8.9% of oiled marshes and associated habitats. One year after the spill began, oil remained on 847 km of

shoreline; two years later, oil remained on 687 km, though at a much lesser degree. Shorelines characterized as heavily oiled decreased from a maximum of 360 km in the most intense oiling phase and down to 22.4 km one year later, and to 6.4 km after two years.

Allan et al. (2012) used passive samplers to monitor PAH levels in shallow water (depth 2-8 m) at four beaches: Grand Isle (LA), Gulfport (MS), Gulf Shores (AL) and Gulf Breeze (FL). In comparison to pre-oiling levels in May 2010 levels of PAHs were significantly increased after the oiling events, but had returned to pre-oiling concentrations at all sites by March 2011, although an increase was found in AL in summer of 2011, possibly due to residual oil leaking from sediments. Kostka et al. (2011) conducted one of the first studies of the *in situ* response of bacterial communities to oil contamination in Gulf beach sands. Similar to the water column, indigenous bacteria were found to be active in degrading the oil. The microbial community structure showed a clear change, with oil-degrading strains dominant. Members of the Gammaproteobacteria e.g., *Alcanivorax* and *Marinobacter*, and Alphaproteobacteria e.g., Rhodobacteraceae, were key players in oil degradation. Overholt et al. (2013) isolated 10 proteobacterial strains (belonging to *Alpha* and *Gamma proteobacteria*) from beaches contaminated with crude oil, and identified multiple putative genes belonging to HC degradation pathways. Also the studies of Newton et al. (2013), Lamendella et al. (2014) and Engel & Gupta (2014) demonstrated significant shifts towards oil degraders in the microbial communities on oiled beach sediments. The coastal sediment bacterial community structure response was further characterized in the mesocosm study conducted by Koo et al. (2014). Kappell et al. (2014) used mesocosms to study the PAH degradation capacity of bacterial communities obtained from heavily oiled and non-oiled beaches. After spiking mesocosms with a mix of naphthalene, fluorene and benzo[a]pyrene, there was a rapid depletion of the first two PAHs, while benzo[a]pyrene was not degraded by either microbial community. Sammarco et al. (2013) examined the distribution and concentrations of TPH and PAH in coastal sediment, seawater, biota, and seafood in NGOM during and after the spill and found oil-derived compounds in varying concentrations in all media. The paper was criticized by Wilson et al. (2014) concerning selection of stations, sampling and analytical methods, data treatment, and the pooling of data. In response, Sammarco et al. (2014) agreed that the methods used were not in accordance with a strict scientific method, i.e. controls should have been included.

Weathered oil appeared at several beach locations as aggregated oily materials often referred to as tar mats or tar balls, the latter is often referred to as surface residue balls (SRBs). A number of studies have characterized the chemical composition of tar balls collected at different locations and time-points after the DWH oil spill, e.g., (Dalyander et al., 2014; Elango et al., 2014; Hayworth et al., 2015; Kiruri et al., 2013; Mulabagal et al., 2013; Singh et al., 2012; Urbano et al., 2013; White et al., 2014; Wise et al.,

2014b; Yin et al., 2015). On AL beaches, the white sand made the oil very visible and prompted various clean-up activities (Hayworth et al., 2011). Cleanup efforts were effective in removing large tar mats, whereas buried tar mats and smaller oil fragments were more difficult to find and remove. In Nov 2011, there was still remnant oil at these locations primarily in the form of large, discontinuous tar mats a few millimeters to several centimeters thick buried under a few centimeters up to nearly a meter of sand. Dalyander et al. (2014) used a numerical model to describe the mobility and redistribution patterns of SRBs that formed in the surf zone at AL and western FL coasts. The SRBs, that typically were oil-free at the surface but with an oily core, moved along the shore, and caused re-oiling of beaches even three years after the initial oil stranding, especially in connection with heavy weather conditions when buried SRBs were re-exposed. Kiruri et al. (2013) found that tar balls contained persistent asphaltene radical species characteristic of crude oil, as well as other radicals that resulted from the weathering process, and were similar to semiquinone-type, environmentally-persistent free radicals that also can be found in contaminated soils. The most persistent and recalcitrant components of the HC mixture may remain for a long time at oil affected beach environments. Gros et al. (2014) studied the weathered HC mixture remaining in beach sand at four oil affected shore locations in FL, LA, MI and AL up to 19 months after the spill, with a particular attention to groups of >n-C22 saturates. They concluded that susceptibility to biodegradation decreased in the order: n-alkanes > methylalkanes and alkylcyclopentanes + alkyl-cyclohexanes > cyclic and acyclic isoprenoids. Aeppli et al. (2012) studied the formation of recalcitrant oil residues in different oiled materials (slicks, sand, rocks) collected over 18 months and found a weathering-dependent increase of recalcitrant oxyhydrocarbons (average molecular formula $(C_5H_7O)n$) ultimately comprising >50% of the solvent-extractable HC residues. Urbano & Elango et al. (2014; 2013) studied the biogeochemistry and biodegradation of SBRs collected along beaches in LA and found that the position at the beach from where aggregates were obtained significantly influenced their composition as well as their susceptibility to biodegradation. Supratidal SRBs were smaller and had lower moisture content and salinity (<2 ppt), whereas intertidal SRBs were hypersaline, had higher N and sulfate concentrations, and contained more crude oil residues and PAHs, dominated by C1- and C2-phenanthrenes, and C2- and C3-dibenzothiophenes. Also microbial populations in SRBs varied with position on the beach and changes in composition ratios over time in the supratidal SRBs were consistent with a biodegradation process partly due to *Mycobacterium* sp. adapted to these conditions. Tao et al. (2011) reported up to a 100x increase in human pathogenic bacteria *Vibrio vulnificus* in tar balls at oiled areas as compared to water samples from the same locations, suggesting that tar balls can act as reservoirs for human pathogens. This was supported by Stephens et al. (2013) who also found a significant increase in *V. vulnificus* density in oil contaminated water samples, although an opposite decreasing effect was observed for another potentially pathogenic

vibrio type *V. parahaemolyticus* in the oil affected water samples. A negative correlation between oil and *V. parahaemolyticus* density was also reported by Smith et al. (2012).

The coast of NGOM is dominated by large salt marshes, such as in Barataria Bay and Terrebonne Bay in LA, and a number of studies have assessed how these salt marsh ecosystems coped with the oiling stress, e.g., (Khanna et al., 2013; Kokaly et al., 2013; Lin and Mendelssohn, 2012; Mahmoudi et al., 2013; Rozas et al., 2014). Studies in marsh sediments collected from multiple sites in LA just before the DWH oil arrived in May 2010 and until June 2013 demonstrated that the oiling increased petroleum alkanes and PAH levels in marshes in average >600 and >180 times, respectively, in comparison to the pre-spill values (Turner et al., 2014a; Turner et al., 2014b), and the recovery trajectory indicates that pre-spill baseline levels most likely would be reestablished by the end of 2015. Hatch (2013) measured PAH concentrations in sediment cores from marshes with various degrees of oiling. Bay Jimmy (LA) was significantly affected, as indicated by TPAH concentrations up to 21,913 ng/g, clearly above the benchmark concentration at which adverse biological effects are thought to occur (i.e., 4,022 ng/g). At heavily affected locations the oil was quickly mixed into salt marsh sediments, with demonstrable effects on foraminifera (see study by Brunner et al. (2013) later). As most of the sampled sites were in a net erosional state that was linked to the presence of oil, oil trapped in salt marsh sediments was deemed to pose an ongoing threat to marsh stability.

A study by Beazley et al. (2012) showed how the microbial community of an oiled salt marsh shifted with the relative richness and abundance of HC-degrading bacteria phyla, such as proteobacteria, bacteroidetes, and actinobacteria, increased in HC-contaminated sediments and decreased again once HCs were below detection. Sediment microbes in oiled salt marshes of Barataria Bay were studied by Mahmoudi et al. (2013) during the first 18 months following the DWH spill at the same stations as studied by Silliman et al. (2012) (see later). Concentrations of alkanes and PAHs at oiled sites decreased significantly over this period, in part due to microbial biodegradation. Petroleum-derived carbon was a primary carbon source for the microbial communities at oiled sites. Bacterial community structure changed after the intrusion of oil, although this change was not as strong as reported previously. The conclusion was that *in situ* biodegradation by indigenous microbial communities contributed to oil degradation and remediation of severely-oiled marsh sediments, and that these sediments have a considerable biodegradation potential. The effects of oiling on salt marsh erosion were studied by McClenachan and collaborators (2013) who found that the heavy oiling significantly weakened the bottom layer of soil, suggesting that the oiled marshes have an increased susceptibility of erosion caused by waves and tidal action. The authors suggested that there is a threshold oil concentration above which soil parameters change dramatically with

a relatively small increase in oil concentration in the soil, and that coastal marshes are not as resilient to large disturbances as previously thought.

Pendergraft et al. (2013) described a novel screening method for measuring PAHs as a proxy for oil in marsh sediments, employing a ramped pyrolysis carbon isotope technique, and demonstrated the use of the method with surface and subsurface intertidal zone sediments from the Barataria Bay area, LA, collected 535 days after the DWH accident. An efficient restoration processes in oil-contaminated salt marsh sediments relies on an adequate supply of oxygen but also indigenous anaerobic bacteria (in particular sulfate-reducing bacteria) can contribute significantly in oxygen-depleted subsurface marsh sediments, as suggested by Boopathy et al. (2012) and Natter et al. (2012). Possible stimulation of microbial oil biodegradation at beaches and other oiled coastal habitats was addressed by several studies. Horel et al. (2012) demonstrated that the HC biodegradation rates in oiled sandy beach environments can be doubled by adding inorganic nutrients. In a subsequent study, Horel et al. (2014b) reported a comparable positive effect on oil biodegradation rates in sandy environments by adding small amounts of organic matter originating from plant or fish materials. An accelerated HC mineralization rate in oiled sandy environments (76% increase) after adding organic fertilizers was also observed by Mortazavi et al. (2013).

Low-trophic ecological effects in coastal communities
A number of field studies have been performed to study the effects and recovery of oiling in marsh vegetation, e.g., (Fleeger et al., 2015; Khanna et al., 2013; McClenachan et al., 2013; Mishra et al., 2012; Silliman et al., 2012; Wu et al., 2012; Zengel et al., 2015). In oil-affected salt marshes, onsite response activities included the placing of booms adjacent to shorelines to prevent oil from reaching shorelines; flushing marsh surfaces with water; cutting and raking marsh vegetation; removing wrack and vegetation; raking heavy oil deposits from soil surfaces; and placing loose sorbent materials. According to Zengel et al. (2015) heavy oiled marsh areas that were not treated showed negative effects on marsh vegetation, intertidal invertebrate communities, and erosion tendency also in 2012, two years after the oiling event. However, the same study found that mechanical treatment could cause additional negative effects by mixing oil into the marsh soils and further accelerate erosion, suggesting that areas suffering only mild oiling were better off without treatment. Fleeger et al. (2015) found the post spill recovery of salt marsh benthic microalgae and meiofauna communities was strongly linked to recovery of *Spartina alterniflora*, and they proposed that this marsh plant could be used as a good indicator for the broader recovery of salt marsh infaunal benthos. For improved airborne monitoring of oiling and oil vegetation stress in salt marshes several field studies demonstrated the use of AVIRIS (Airborne Visible/InfraRed Imaging Spectrometer) data collected from low and medium altitudes (Khanna et al., 2013; Kokaly et al., 2013;

Peterson et al., 2015). Areas denuded of vegetation by the spill showed varying degrees of re-vegetation in the following year, with poorest recovery on the seaward edge of affected marshes. However, the studies largely found that affected marshes seemed to recover rather rapidly although some heavily oiled areas were characterized by oil-driven plant death, increased erosion and permanent marsh area loss. Several mesocosm studies have been conducted to characterize the impact of DWH oiling on different species of marsh plants in a controlled manner, e.g., (Anderson and Hess, 2012; Caudle and Maricle, 2014; Horel et al., 2014a; Judy, 2013; Judy et al., 2014; Langley et al., 2015; Lin and Mendelssohn, 2012). The studies demonstrated variable susceptibility to oil among different marsh species, but noted that negative effects typically became significant if the oil managed to penetrate the marsh soil. Several studies found that marsh vegetation, and in particular the ability of the marsh plants to maintain their root growth, was a key factor for the microbial oil biodegradation process in affected marshes. Thus, fertilization strategies that maximize marsh plant root growth will be the most effective at increasing the microbial degradation of oil and will have the greatest potential to mitigate the impacts of oil in marsh ecosystems.

Response measures for reducing the quantity of oiling of marshes, wetland and estuaries included construction of barrier sand berms, the restriction or blocking of inlets, and the diversion of freshwater from rivers to the coastal marshes and into the ocean, in order to flush away the oil. The study by Martínez et al (2011) noted that these measures may have resulted in long-term negative changes to the ecosystems that they were intended to protect, including changing hydrological and ecological characteristics of estuaries, altering sediment transport along the coastal barrier islands, causing loss of sand resources, and adversely impacting benthic and pelagic organisms.

Data on effects of the DWH oil spill on seagrass communities are largely absent from the research literature, although seagrasses are important habitats for many marine species and NGOM has more than 50 percent of the total U.S. distribution of seagrasses. The seagrass beds within the Chandeleur Islands area constitute the largest continuous seagrass bed in NGOM and are particularly valuable. According to the DWH oil spill damage assessment report, 109 hectares (1.09 km^2) of seagrass beds in the Chandeleur Islands area were destroyed during the DWH oil spill.

Significant shifts in benthic microbial eukaryote communities in response to oiling in coastal sediments were reported by Bik et al. (2012). In a study at Dauphin Island and Mobile Bay, AL, they found that diverse pre-spill assemblages of Metazoa were replaced by less diverse post-spill communities dominated by HC degrading fungal species. A rich assemblage of nematode species in pre-spill sediments was replaced by post-spill communities dominated by predatory and scavenger species alongside an abundance of juveniles. A study performed by Brunner et al. (2013) focused on sediment foraminifera from oiled marshes in Mississippi Sound, Chandeleur Sound, and Barataria Bay and found that the oil caused adverse

effects in foraminifera cell membranes, reproduction capability, pseudopodial activity and mortality rate (at the most heavily oiled locations); although some positive population effects were observed at some lightly oiled sites.

Shallow-water corals

Large areas in the NGOM have water depths between 30 and 100 m which are habitat for shallow water corals. Shallow water corals can be distinguished from deep-sea corals by their sharp coloration that originates from symbiotic and photosynthetic zooxanthellae (unicellular dinoflagellate algae) within the coral tissues. Corals are found as nearshore rocky reefs or as larger mesophotic coral ecosystems (MCEs) along the edge of the shelf. Highest coral density is found in the FL shelf area, an area that was mildly affected by the DWH oil spill. At least four well-known MCEs are documented in the northeastern and eastern parts of NGOM; the Flower Garden Banks National Marine Sanctuary off the coast of TX, the Pinnacles Trend area off AL, the FL Middle Ground reef system, and the Pulley Ridge reef east of the FL Keys (Locker et al., 2010). The reefs in Pinnacles Trend were situated below oil-slicks for several weeks and, in addition, dispersants were added to oil slicks in this area. Etnoyer et al. (2015a; 2015b) found evidence that the oil spill caused injury to at least four species of gorgonian octocoral sea-fans in the Pinnacles Trend area, in the form of eroded polyps, discoloration, bare branches, overgrowth, missing branches, and broken branches. By comparing ROV pictures taken of the same colonies before and after the spill, a severe decline of coral condition was found; large colonies displaying injuries increased from 4-9 % before 2003 to 38-50 % in 2011. It is a challenge to conduct controllable exposure effect studies on fully grown coral colonies, but Goodbody-Gringley et al. (2013) developed a bioassay using larvae of the stony corals *Porites astreoides* and *Montastraea faveolata* (currently: *Orbicella faveolata*), to study the effect of DWH oil (crude, weathered and WAF) in combination with the Corexit dispersant (CEWAF), and dispersant alone under laboratory conditions. These coral species live in shallow waters and can be found off the TX coast as well as in the FL Keys. Settlement and survival of larvae of both species decreased significantly with increasing concentrations of crude oil, weathered oil, WAF, CEWAF, and dispersant; indicating that oil spills such as DWH had the potential to impact the settlement and survival of coral larvae, thereby affecting the resilience and recovery of coral reefs following exposure to oil and dispersants.

Coastal invertebrates

Studies of the effects of DWH oil (and also oil + dispersants) on different bottom-dwelling invertebrate groups living in coastal habitats have to a large extent been based on laboratory experiments and toxicity tests, with test results often provided in technical reports, which were not examined for this review. Burrowing invertebrates, such as polychaetes and amphipods, are highly abundant in coastal shallow-

waters and wetlands and are prey for many predators inhabiting the NGOM coastline. Testing of oil toxicity to the estuarine burrowing amphipod *Leptocheirus plumulosus* demonstrated increased toxicity at concentrations observed in coastal sediments following the DWH spill (Krasnec et al., 2015). Rozas et al. (2014) used field mesocosms containing oiled sediments in northern Barataria Bay to study effects on growth rate of juveniles of panaeid brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*). Reduction in growth rates was observed at the most severely oiled sites where brown shrimp grew at less than half the rate of un-exposed shrimp; correlating to concentrations of PAHs in sediments. The same shrimp species were studied by van der Ham and de Mutsert (2014), who found that shrimp abundance (and partly also shrimp size) increased within oil affected estuaries. The authors suggest exposure to PAHs may have reduced growth rate, resulting in a delayed movement of shrimp to offshore habitats and an increase of within-estuary shrimp abundance, or that fishing closures established after the spill led to increased shrimp abundance.

Field studies by Grey et al.(2015) detected no significant effect of oiling on megalopal settlement or body weight of blue crab (*Callinectes sapidus*) one year post spill, but the study was hampered by high unexplained variation. An experimental study in blue crab by Alloy et al. (2015) found that survival of crab larvae exposed to oil WAF in combination with natural sunlight was influenced by both factors, indicating the larvae to be sensitive to photo-induced oil toxicity. The concentration of PAH in the test media in that study was comparable to levels reported in the NGOM during the DWH spill. Pie et al (2015) performed a 31 d test with juvenile blue crabs exposed to weathered oil in field-collected sediments, with the most contaminated sediments having oil-derived TPAH levels of more than 2 million ppb (i.e. 2 parts per thousand), but without finding any significant effect of TPAH levels on mortality, growth, ecdysis or on a suite of molecular effect biomarkers [including comet assay, Cu-metallothionein gene expression, glutathione-S-transferase (GST), and manganese superoxide dismutase (MnSOD)] analyzed in the test crab. Unfortunately, the study did not include markers that could confirm any PAH uptake, such as analyses of PAH metabolites in crab urine or haemolymph, which could have revealed whether sediment bound PAHs to any measurable extent was taken up by the crabs under the test conditions used. Several other studies with coastal crustaceans have focused on issues that mostly relate to dispersants, e.g., (Anderson et al., 2014; Anderson Lively and McKenzie, 2014; Chase et al., 2013; Hemmer et al., 2011; Pie and Mitchelmore, 2015), and because dispersants were not used near the coast they fall largely outside the scope of the present review.

Coastal filter feeders, such as barnacles (*Balanus sp.*), marsh mussels (*Geukensia demissa*), coquina clams (*Donax spp.*) and oysters (*Crassostrea virginica*) were expected to accumulate chemical contaminants at locations affected by the DWH oil spill, both by direct uptake and indirectly via diet. Fry & Anderson

(2014) used natural radiocarbon tracing to test the hypothesis that bacteria were a source of oil carbon for estuarine barnacles and marsh mussels in Barataria Bay estuary during the spill. However, no evidence for significant oil carbon uptake was found. Corroborating observations of oysters displaying no significant oil carbon uptake in oil affected coastal areas were reported by several other field studies, e.g., Soniat et al. (2011), Carmichael et al. (2012b), Xia et al. (2012). Snyder et al. (2014a; 2014b) measured oil spill related PAHs in samples of sand and coquina clams from oiled FL Panhandle beaches. They found that both types of samples displayed decreasing concentrations post spill, reaching undetectable levels within one and two years after oiling, respectively.

Fish in coastal habitats

Concerns about the potential effects of the DWH spill on seafood and fish production were greatest in the nearshore habitats of NGOM (up to 200 m depth) which support a rich diversity of fish species. Xia et al. (2012) monitored PAH levels in seafood (fishes, shrimps, crabs, oysters) from oil affected areas at the MI coast from May 2010 to August 2011 and found statistically higher levels of TPAHs in all four types of seafood samples during the early part of period (May-Aug 2010) compared to the later months. Although PAHs were detected, all tested samples were below public health levels of concern. Within one year of the spill, concentrations in all samples were well below public health limits established by NOAA, the FDA, and Gulf Coast states (Xia et al., 2012; Ylitalo et al., 2012). Similarly, TPAH concentrations in Gulf menhaden (*Brevoortia patronus*) from coastal LA declined about 2-fold from 2011 (6.0-7.4 µg/g) to 2013 (3.2-4.1 ng/g) assessed in whole fish samples, while BaP carcinogenic equivalents declined from 75.4 to 1.7 ng/g (Olson et al., 2016).

The acute effects on early-stage survival of fish inhabiting seagrass nursery habitat were assessed by reference to a five-year data set (2006–2010) of 853 individual trawl samples from 12 stations between MI and FL. Within the oil-affected region, there were no shifts in species composition following the spill, and immediate losses of 2010 cohorts were not evident, even for 6 of 20 abundant species at moderate to high risk of oil exposure (Fodrie and Heck, 2011). For commercial species, higher catch rates following the spill were likely due to fisheries closures (Fodrie and Heck, 2011; Schaefer et al., 2016). Similarly, there were no significant differences in recruitment of marsh-associated resident and transient nekton in AL salt marshes following the DWH spill (Moody et al., 2013). There was also little effect of the spill on recruitment of red snapper (*Lutjanus campechanus*) to multiple artificial reefs in NGOM (Szedlmayer and Mudrak, 2014). In 2010 and 2011, there were no year-class failures, and age-0 class abundance was determined primarily by the presence of age-1 individuals and concentrations of dissolved oxygen. However, the trophic position of snapper captured at natural and artificial reefs increased following the

spill, consistent with a dietary shift from zooplankton and reported spill impacts on zooplankton populations (Tarnecki and Patterson, 2015).

According to Murawski et al. (2014), increased bile PAH metabolites in red snapper supported links between oil exposure and a higher prevalence of unusual skin lesions in the vicinity of the DWH site. In 2011, the lesion prevalence was tentatively correlated to PAH exposure markers but not to surface salinity, temperature anomalies, or known epizootics. Unusual external lesions on red snapper from NGOM were associated with fish pathogens (*Photobacterium damselae; Vibrio vulnificus*) isolated from affected fish. However, RNA gene sequencing demonstrated that both pathogens were part of the normal microbiota of healthy red snapper, indicating that pathogens recovered in previous studies were not lesion-forming (Arias et al., 2013). The proposed association between the prevalence of lesions and the oil spill assumed that oil-exposed fish were immunocompromised and sensitive to opportunistic pathogens. However, evidence of immuno-toxicity in fish was mixed. Between oiled and un-oiled sites, there were no obvious changes in peripheral blood leukocytes and splenic melano-macrophage centers (SMCs) of alligator gar (*Atractosteus spatula*). In contrast, decreased lymphocyte counts and increased numbers of SMCs were evident in Gulf killifish (*Fundulus grandis*) and sea trout (*Cynoscion nebulosus*), in parallel with CYP1A induction in the trout, suggesting a link to oil exposure (Ali et al., 2014). Although causal links between oil exposure and the prevalence of skin lesions could not be proven, neither could the null hypothesis of no relationship be accepted. Nevertheless, a 53% decline in prevalence and severity of lesions from 2011 to 2012, in parallel with an apparent lower exposure to oil, was consistent with a causal hypothesis.

Lab experiments with fish demonstrated a variety of responses to oil. The acute toxicity of South Louisiana crude to juvenile killifish was influenced by weathering, chemical dispersion, and salinity, but unrelated to PAH concentrations (Kuhl et al., 2013). After 1 and 4 weeks of weathering in laboratory microcosms at 4, 12, and 18 ppt salinity, CEWAF and dispersant remained acutely toxic at 4 ppt salinity, in contrast to a loss of toxicity after 16 weeks at higher salinities, suggesting a salinity interaction with rates of oil degradation and toxicity. Compared to normal oxic conditions, the survival of larval sheepshead minnow (*Cyprinodon variegatus*) was dramatically reduced by 48 h co-exposures to hypoxia and CEWAF of MC252 oil or Corexit® 9500A (Dasgupta et al., 2015); WAF was not lethal under any condition. Thus, oil spill impacts may be potentiated in areas in NGOM subject to annual periods of oxygen depletion. Adult Gulf killifish exposed to WAFs of crude oil showed evidence of exposure to PAHs (CYP1A induction) and of oxidative stress (increased serum antioxidant capacity) (Crowe et al., 2014). Similarly, oil collected from the collapsed DWH riser pipe caused sublethal responses in larval and juvenile spotted seatrout in lab studies. Four-day exposures to high energy WAF (HEWAF), CEWAF, or dispersant alone, increased the expression of *cyp1a* genes, in association with growth depression (Brewton

et al., 2013). Larval seatrout were affected most by CEWAF, while juveniles were affected more by HEWAF. The results suggest potential impacts on productivity of exposed sea trout, and a need for monitoring fish production in oil affected coastal ecosystems.

Changes in gene expression of Gulf killifish sampled from oiled marshes indicated exposure to oil (e.g., up-regulation of *cyp1a*), toxicity (e.g., gill pathology) and reproductive impairment for more than one year after the landfall of oil, despite very low concentrations of hydrocarbons in water and tissues (Dubansky et al., 2013; Whitehead et al., 2012). These responses to DWH oil were replicated in laboratory studies of adult (Pilcher et al., 2014) and larval killifish (Whitehead et al., 2012), and inland silversides (*Menidia beryllina*) (Adeyemo et al., 2015). Effects on embryos mirrored the toxicity of DWH WAF to zebrafish embryos (Incardona et al., 2013), and included changes to gene expression indicative of PAH accumulation and potential effects on sex determination, sexual differentiation, and growth regulation. In adult killifish, high concentrations of WAF caused transcriptional responses predictive of effects at severely-oiled locations, including DNA damage. Low concentrations affected expression of genes associated with regulation of transcription, cell cycle progression, RNA processing, DNA damage, and apoptosis (Pilcher et al., 2014). In killifish sampled from oil-contaminated sites between TX and FL, 1070 genes were down-regulated, while 1251 were up-regulated (Garcia et al., 2012), suggesting a complex response to the accumulated hydrocarbons. Similarly, exposure to DWH oil damaged DNA and DNA repair systems and impaired the immune system of shovelnose sturgeon, *Scaphirhynchus platorynchus*, which was used as a surrogate for the endangered Gulf sturgeon (*Acipenser oxyrinchus desotoi*) (DWH-NRDA, 2015). Overall, gene expression in fish was a robust indicator of oil exposure, potential impairment of normal cell function, and DNA damage.

Residual oil in sediments may impair fish production. Sediments spiked with lab-weathered Louisiana crude, and oiled sediments collected from Barataria Bay, LA in December, 2010 caused developmental malformations in embryos of zebrafish at sediment TPAH concentrations of 27 mg /kg d.w. (normalized to 1% organic carbon), but not at 2 mg/kg (Raimondo et al., 2014). Concentrations above 78 mg/kg caused nearly complete embryo mortality, indicating that sediment contamination could reduce recruitment. However, the toxicity of spiked sediments stored for 40 days at 4°C decreased by nearly 10-fold, suggesting loss of lethal components. Developmental defects typical of DWH oil toxicity (de Soysa et al., 2012; Incardona et al., 2013) were evident in killifish embryos exposed to sediments collected from oiled marshes at Grand Terre, LA. Compared to controls, exposed embryos failed to hatch or were smaller, showed signs of decreased vitality, and suffered from pericardial and yolk sac edema; CYP1A induction in multiple tissues indicated PAH accumulation (Dubansky et al., 2013). Reference sediments sampled from AL marshes and spiked with weathered MC252 were lethal to juvenile southern flounder

(*Paralichthys lethostigma*) during 30-day exposures at TPAH concentrations greater than 10 mg/kg (LC20 = 36.3 mg/kg) (Brown-Peterson et al., 2015). Growth of survivors and hepatosomatic indices were reduced and the prevalence and severity of histopathological changes were increased at EC20s ranging from 0.29 to 26.7 mg/kg TPAH in association with activation of *cyp1a* genes and a shift in commensal bacterial populations of the gut. Overall, exposure of fish to oil-contaminated sediments reduced fitness and increased the potential for population-level impacts. There have been no field studies of population impacts related to sediment contamination (Pearson, 2014), so experimental data remain the strongest basis for assessing potential effects (Dubansky et al., 2014).

2.4 Effects in long-lived marine tetrapod vertebrates

Birds

The NGOM region is crucial to many local shorebird populations as well as to many migrating bird species breeding in areas far from the Gulf, and shorebirds were the most affected tetrapod vertebrates during the DWH spill, showing a steep increase in mortality rates (Antonio et al., 2011). Species like laughing gull and brown pelican were seriously affected (Tran et al., 2014). According to estimates by Henkel et al. (2012), it is possible that more than one million migratory shorebirds representing 28 species were exposed to some degree to DWH oil during their 2010–2011 non-breeding season. Approximately 8.6% of shorebirds trapped from fall 2010 to spring 2011 showed visible signs of oiling. Exposure to oil may affect shorebirds through direct acute mortality as well as indirectly or long term by sub-lethal effects on bird health and behaviour. Habitat degradation may affect bird populations in ways that carry over to subsequent seasons. In two studies, Haney et al. (2014a; 2014b) used a carcass sampling model and an exposure probability model to estimate that the coastal bird kills during DWH could potentially have been as high as 600-800 thousand individuals, with the species most affected being laughing gull *Leucophaeus atricilla* (32% of NGOM population killed), royal tern *Thalasseus maximus* (15%), brown pelican *Pelecanus occidentalis* (12%) and northern gannet *Morus bassanus* (8%). The study was criticized by Sackmann and Becker (2015) who suggested that an underestimating of carcass transport probability to shorelines was leading to overestimation of bird deaths by an order of magnitude; a comment which was refuted in a response letter from Haney et al. (2015).

Walter et al. (2014) assessed the demographic trends of brown pelicans in LA before and after the DWH spill by banding 1114 individuals on LA barrier islands from 2007 to 2009 and tracking their distribution via band re-sighting surveys from 2008 to 2011. The study found little age-variation within the population that could readily be assigned to spill-related mortality, which was contrary to expectations. Other coastal bird species in NGOM that have been studied after the spill include northern gannet *Morus bassanus* (high oiling rate observed) (Montevecchi et al., 2012), North America loon *Gavia immer* (low but increased

PAH concentrations in blood in 2012 indicate contaminated feed) (Paruk et al., 2014), dunlins *Calidris alpina* (100,000 individuals could have been affected by DWH oil, population also disturbed by beach clean-up) (Henkel et al., 2014). A study on the Canadian breeding population level of northern gannets, which partly over-winter in the northern Gulf area, found that their abundance and reproductive success had declined recently (Franci et al., 2014), but the study could not link this effect to the DWH oil spill or to differences in reproductive hormonal status in breeding birds returning from NGOM. It is difficult to interpret the significance of these observations without knowing the recovery rates of gannets after sublethal exposures to oil. Finch et al. (2011) investigated bird embryo toxicity of weathered DWH oil in mallard duck *Anas platyrhynchos* by painting varying amounts of oil on the surface of eggs, and found that the mortality of duck embryos occurred as early as day 7 of development and the median lethal dose of weathered crude oil was about 30 mg/egg (or 0.5 mg/g egg). Also the effect of oil dispersant (Wooten et al., 2012) and the combined effect of oil and dispersants were investigated in this way (Finch et al., 2012; Finch et al., 2011; Wooten et al., 2012), partly demonstrating increased toxicity when oil dispersants were present.

Sea turtles

Increased sea turtle mortality was observed after an initial delay during the DWH oil spill (Antonio et al., 2011). Five kinds of sea turtles occur in NGOM; the leatherback (*Dermochelys coriacea*), loggerhead (*Caretta caretta*), green sea turtle (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and Kemp's ridley (*Lepidochelys kempii*), the latter is particularly vulnerable as it nests only in the Gulf of Mexico. In addition, several brackish water turtle species occur in salt marshes along the gulf coast. Only a handful of papers addressing sea turtles have been published after the DWH event, i.e. (Barron, 2012; Drabeck et al., 2014; Follett et al., 2013; Hart et al., 2014; Lamont et al., 2012). Sea turtles are long lived creatures and studies to assess conditions of stress in individuals and populations are both technically and ethically challenging. Data from NOAA indicates that sea turtle stranding rates increased significantly (possibly 5x) after the DWH oil spill. Population characterization studies, such as the one done by Avens et al. (2012) for NGOM green turtles, provide necessary background data for assessing the long term effect of large perturbations such as the DWH spill. Foraging areas used by loggerheads in the northern Gulf were characterized by Hart et al. (2014) from satellite tracking of 59 tagged loggerhead individuals between 2010 and 2013. Loggerhead foraging sites were found to overlap with the footprint of the DWH oil spill, but also with trawling activities and ongoing oil and gas extraction activities. Of the tracked loggerheads, 32% took up residence year-round within the foraging habitats of the NGOM, indicating the DWH oil spill could have a more far-reaching effect for this turtle species than previously believed. Significant declines in reproductive parameters of loggerheads in the NGOM were reported by Lamont et al. (2012), and although the study could not establish any direct link to the DWH oil spill, it highlighted the potential

risks of oil spills to an already stressed sea turtle population within the NGOM area. Drabeck et al. (2014) studied markers of oil exposure in blood plasma from brackish water diamondback terrapin turtles (*Malaclemys terrapin pileata*) in LA salt marshes. Low concentrations of contaminants were found that were roughly aligned with the extent of oiling at the sampled sites, but the authors suggest that additional background data and further analyses of more appropriate matrices (liver or fat) were needed to assess the degree of exposure.

Marine mammals

More than 20 species of whales and dolphins and one species of manatee occur in NGOM, and all are protected under the USA Marine Mammal Protection Act (MMPA). Six species are listed as endangered under the Endangered Species Act (ESA) (Campagna et al., 2011). For sea mammals, increased mortality rates were observed after an initial delay, but pre-spill data seem to indicate that the observed growth in the mortality rate was not entirely a consequence of the DWH spill (Antonio et al., 2011). For cetaceans, Williams et al. (2011) estimated that the carcasses recovery rates may, on average, have been as low as 2% (range: 0-6.2%) of the actual cetacean deaths, suggesting that mortality after the DWH spill may have been severely underestimated.

An unusual mortality event (UME) involving primarily bottlenose dolphins (*Tursiops truncatus*) in LA started in February 2010 and continued and expanded to MI and AL during and after DWH. As the UME was ongoing in September 2014, Litz et al. (2014) suggested that the DWH oil spill could have prolonged and expanded the UME, although it certainly was initiated by other factors. Carmichael et al. (2012a) reported that an unusually high number (186 individuals) of near-term and neonatal bottlenose dolphin mortalities occurred in the northern Gulf in 2011, and speculated that increased stress from bacterial infections and depleted food resources or other factors could be the cause. Schwacke et al. (2014a) reported that live bottlenose dolphins examined during 2011 in Barataria Bay (BB), LA, suffered from adrenal disease, lung disease, and poor health conditions that likely were linked to oil exposure from the DWH spill. Comparing examination results of BB dolphins with individuals from the unoiled Sarasota Bay (SB), FL, showed several uncommon disease conditions in dolphins from BB. One example was hypoadrenocorticism, a condition consistent with adrenal toxicity and previously reported for oil-exposed laboratory mammals. Compared to SB dolphins, the BB dolphins were estimated to be five times more likely to have moderate to severe lung disease, characterized by significant alveolar interstitial syndrome, lung masses, and pulmonary consolidation. Of 29 BB dolphins, 48% were given a guarded or worse prognosis, and 17% were considered poor or grave, i.e., they were not expected to survive. Disease prevalences in BB dolphins were significantly greater and more severe than in SB dolphins, and greater than previously reported in other wild dolphin populations. The authors later published a letter (Schwacke

et al., 2014b) to correct some minor errors in the paper. Further evidence for a possible link between compromised health status in dolphins and the DWH oil spill was provided by Venn-Watson et al. (2015) who examined adrenal gland and lung lesions in 46 fresh non-perinatal bottlenose dolphin carcasses stranded between June 2010 and Dec 2012 in LA (including 22 from BB), MI and AL, inside the UME area. By comparing the necropsy results with similar data from 106 dolphins stranded outside the UME area they found that the UME dolphins were more likely to have primary bacterial pneumonia (22% compared to 2% in non-UME dolphins, P = .003) and thin adrenal cortices (33% compared to 7% in non-UME dolphins, P = .003). In 70% of UME dolphins that suffered from primary bacterial pneumonia, the condition either caused or contributed significantly to death, and the authors suggested that elevated exposure to petroleum compounds originating from the DWH spill had contributed to the observed decreased health conditions of dolphins within the UME area. Van Dolah et al. (2015) used transcriptomics of skin biopsies to assess dolphin health condition in the UME area, but without finding any links to possible contamination stress from the DWH spill.

Sperm whales occur in NGOM in all seasons with about 750 individuals being the mean population estimate. Ackleh et al. (2012) observed that the whale density in the area close to the DWH blowout site was decreased (by a factor of 2) after the spill in comparison to the pre-spill situation, but the data was uncertain. Wise et al. (2014a) used skin biopsies collected from NGOM sperm whales to test the toxicity of Corexit 9500 and Corexit 9527 dispersants and found both dispersants to be cytotoxic and genotoxic to whale skin fibroblast cells. In another study with sperm whale skin biopsies, Wise et al. (2014b) investigated genotoxic metal (chromium and nickel) concentrations which they considered to be a possibly understudied aspect of DWH related contamination. They detected metal levels well above expected background, but again the data were highly variable and uncertain.

West Indian manatees (*Trichechus manatus latirostris*) are rare and threatened animals in NGOM and depend on availability of healthy seagrass areas for feeding. In US waters, they are primarily found in the coastal areas of FL, but can occasionally be found as far west as TX. By using a Bayesian modelling approach, Martin et al. (2014) compared the manatee occupancy rate (the proportion of sites occupied by the species) in oil affected and non-oiled areas in NGOM. The method enabled them to estimate the number of manatees potentially present in the oil contaminated area. However, according to the DWH damage assessment report, no manatees were sighted in oil during the spill although their geographical distribution overlaps with the DWH oil footprint.

A way of describing spatial patterns of injuries and mortality in birds, turtles, and sea mammals during DWH was tested by Follett et al. (2013) by using data on animal sightings (live and dead) combined with oil contamination information (PAH in seawater and sediments) and hydrographic data. The authors

identified a unique pattern of animal deaths during the data collection period, but reliable conclusions regarding cause-and-effect relationships could not be established due to paucity of data. M.G. Barron (2012) discussed the potential immunotoxicity of the DWH oil to sea turtles; marine mammals; and birds. Immunotoxicity in these organisms is not commonly assessed during oil spills, including the DWH oil spill, and this was a significant shortfall according to this author.

3. Overall discussion

For all disciplines covered by this review, the DHW oil spill, like the EVOS, will be regarded in the future as a major "science incubator" due to the amount of money spent on research, the wide array of innovative studies, and the new understanding of oil fate, behaviour and effects, as well as methods for assessing those issues. But although our knowledge about the effects of major oil spills on marine and coastal ecosystems has improved considerably, there are still critical research needs from questions that remain unresolved, are newly recognized, or are poorly known.

Understanding the fate of the oil and gas spilled in connection with the DWH was essential because it determined the degree of exposure and subsequent impacts on the affected organisms and ecosystems downstream (Figure 3). The fate of the released HCs during DWH was influenced by an array of factors; including the great depth, the composition and magnitude of the blowout, the extensive use of dispersants (both deep and surface applied), high sea surface temperature, strong solar irradiation, the presence of a community of indigenous oil degrading microbes, and the oceanic circulation pattern in deep and surface waters during the spill. Several fate studies refer to the assumption that because many natural oil and gas seeps exist in the NGOM, it is uniquely well primed for biodegradation of HCs released in spills. However, there may not be a solid scientific basis for assuming that the HC biodegradation was any more rapid than in oceanic and coastal regions with similar temperature regimes, but without oil seeps. To our knowledge, no studies have presented experimental or observational comparisons with "control" environments to support the theory. In fact, emerging marine metagenomics support the "everything is everywhere" view, suggesting that seed populations of methanogens and other HC degrading microbes can multiply quickly from very low dormancy in any seas above shelf areas, as releases of methane from sediments or sub-seabed reservoirs are virtually ubiquitous along continental margins.

Many fate studies addressed the behaviour of the unprecedented deep plume of oil and gas rich water that spread with deep-sea currents at 1000-1300 m depth, while its constituents underwent transformation and degradation caused by physical and microbial processes. The deep plume stretched out in a predominantly southwest direction, possibly as much as 400 km from the Macondo wellhead (DWH-NRDA, 2015). In deep benthic habitats, it left a chemical signature characterized by increased levels of persistent petrogenic

substances (e.g., hopanes), recalcitrant oil degradation products and patchy depositions of a brown flocculent material (oily marine snow) that increased in intensity with proximity to the Macondo wellhead. Field studies have demonstrated that oily marine snow also formed in oil-rich surface water and facilitated downward transport of oil from the surface to the sea floor. It is likely that the relatively light nature of the Macondo crude, the relatively small droplet size in the initial plume, the low oil concentrations in the deep plume and the presence of an indigenous community of oil degrading bacteria all were factors that contributed to biodegradation of the oil. Chemical constituents of the Corexit mixture were detected at concentrations that appeared to be non-toxic to pelagic microbial communities from the deep sea, although mixtures of oil and dispersants caused major changes in microbial community structure. The presence of dispersants increased the bioavailability of oil and oil HCs, leading to higher exposure and hence increased impacts in the short term. However, the degradation of oil also increased when Corexit was present. Microbial communities in the deep sea were able to break down the constituents of the Corexit dispersant, in line with oil components, although the degradation of the DOSS component of Corexit seemed to be slower than for oil components. Where dispersants were applied, there was an increased formation of oily flocs in surface water.

As deep sea coral colonies can live for hundreds and even thousands of years, they are highly vulnerable to catastrophic events such as DWH. The assumption that fallout of oily flocs from the spill was detrimental to deep sea corals attracted much attention and concern from the research community. Although the deposition of oil flocs was patchy, the intensity increased with proximity to the Macondo wellhead. At one coral site 6 km south of the wellhead, more than 90% of the assessed coral colonies showed sign of injury. As demonstrated by White et al. (2012b), multiple lines of evidence provide a large degree of certainty that observed deep water coral damage is directly related to the DWH oil spill. Deepwater coral sites that have been identified as possibly affected have been monitored several times during and after the DWH spill, and follow-up surveys are expected to continue for years. Surprisingly, the shallow water coral reefs received much less attention than the deep water corals with regard to effect studies after DWH, although the coral rich area of Pinnacles Trend (AL) suffered both severe oiling and possible combined exposure to dispersants that were applied to those oil slicks.

Marine mammals are generally sensitive to oil spills as they are typical of K-selected species; i.e. large size, long-lived species producing few offspring that require long periods of gestation, parental care, and/or sexual maturation. The study of pollution stress in marine mammals is extremely challenging as both technical and/or ethical constraints prohibit the use of experimental manipulations to investigate relationships between exposure, internal dose, and adverse health effect developments. Stranded specimens are an important source of information and biological samples, although research suggests that

only one in every 50 dead marine mammals in NGOM is ever found (Williams et al., 2011). An increased frequency of dolphin strandings in the northern Gulf has been recorded since February 2010 and it is apparently still ongoing. Unprecedented deaths and increased strandings have been interpreted as a possible indicator of the low overall health and condition of local and regional sea mammal populations. Although the dolphin UME (Unusual Mortality Event) started *before* the DWH accident, recent studies have strengthened the evidence for a link between adverse health stress originating from the DWH oil spill and the prolonged duration and expansion of this multi-year UME event, although it most certainly is caused by a complex of factors. However, NOAA has ruled out morbillivirus and marine biotoxins from red tide events as causal agents; two of the most common causes of previous dolphin UMEs in NGOM (Litz et al., 2014). It is thought that exposure to oil spills is a combined stress factor that can reduce the health condition of dolphins, making them more susceptible to pathogens and to cold-water stunning (Schwacke et al., 2014a; Venn-Watson et al., 2015).

The effects of oil spills on sea turtles have many unknowns. It is a significant problem that sea turtles, if killed by oil exposure at sea, are likely to sink. All five kinds of sea turtles that occur in NGOM are listed under the ESA as threatened or endangered. Before the DWH disaster, the green sea turtle, Kemp's ridley sea turtle and the loggerhead sea turtle were already identified as species needing special attention as a result of habitat disturbance and incidental fisheries related mortality. Sea turtles have high mortality rates both at the egg stage, as hatchlings and juveniles, and in many areas as adults. They are relatively old before they start reproducing. Following the DWH spill, a special rescue operation was mounted to transport 25,000 turtle eggs from the Gulf to FLs Atlantic coast (Inkley et al., 2013), a move to lessen the risk for sea turtles to perishing from oil contamination of their nests. Quantifying dead stranded sea turtles is one of the few methods available for assessing stress on a sea turtle population. Sea turtle strandings were at record levels in 2010 and 2011 and continued above normal in 2012 according to the NOAA protection program for sea turtles (http://www.sefsc.noaa.gov/species/turtles/). On average, about 240 sea turtles are found stranded in the NGOM annually, but between May 2010 and November 2012 more than 1,700 strandings were recorded. Most turtles stranded have been the endangered Kemp's ridley sea turtle, which nest only in the GoM. There is a need for more research on how oiling affects sea turtles, particularly about the types and concentrations of chemicals contained in the air directly above an oil spill, because sea turtles (and marine mammals and birds) breathe in close proximity to the seawater-air interface. Similarly, the effects of inhaled or aspirated oil on sea turtles and marine mammals are a matter of great uncertainty.

Seabirds are susceptible to increased rates of mortality if they contact oil, and are usually the most numerous vertebrates found dead following spills. Enumerating dead seabirds is the archetype for

assessing environmental impact of marine oil spills, but assessments using sublethal markers of effects are becoming more common. Reported numbers of dead birds related to the DWH spill varied greatly, indicating a research need to improve and standardize bird mortality models, such as those described by Li et al. (2014) or by (Ogden et al., 2014). Comparison of mortality data to other spills (i.e. EVOS) suggested that effects on regional seabird populations during DWH were comparatively lower, a view supported by post-spill age-distribution surveys, e.g., in brown pelicans. Two main approaches were used to study DWH oil spill effects on birds: field studies of populations, and experimental studies of individuals. In the case of field studies, the DWH event highlighted the critical need for pre-spill data on populations of key seabird species (such as brown pelican). The lack of pre-spill data for pelicans gave a relatively incomplete picture of pelican ecology in NGOM in the period before the DWH spill. The same information shortage applies to other species, such as royal tern and black skimmer (*Rynchops niger*). It is notable that studies so far demonstrate that the presence of dispersants enhanced the toxicity of oil to early life stages of coastal waterbirds.

Much of the research on DWH impacts concerned key shoreline habitats, such as salt marshes, wetlands, estuaries and beaches, and how the restoration process in different shoreline habitats proceeded in the months and years after the spill; several review papers summarize and discuss these issues (Bergeon Burns et al., 2014; DeLaune and Wright, 2011; Fodrie et al., 2014; Joye et al., 2014; Lewis et al., 2011; McGenity, 2014; Mendelssohn et al., 2012; Pennings et al., 2014; Santos et al., 2011). More than 2100 km of shoreline were affected, but the degrees of oiling varied considerably, which also was reflected by the large range of contamination concentrations observed in sediments, or other sample matrices, from different sites (ranging from background levels to severely contaminated). However, at coastal sites where marsh sediments or wetland soils were heavily contaminated, there was not necessarily a corresponding degree of hydrocarbon contamination in living organisms (Fry and Anderson, 2014). Similarly, invertebrates that inhabited obviously oil-polluted habitats appeared in several cases to cope surprisingly well with the oiling (van der Ham and de Mutsert, 2014), although other studies demonstrated reduced growth during the peak of contamination (Rozas et al., 2014). Salt marsh vegetation forms the base of nearshore food webs, providing both primary production nutrients and key habitats for many organisms. Negative effects on marsh plants can therefore initiate a cascade of impacts to organisms at higher trophic levels. In the laboratory, oil exposure caused detrimental effects on salt-marsh plants, although field studies tended to indicate a high degree of marsh plant resilience to oiling, especially if the oil did not penetrate into the sediment. The review of DeLaune and Wright (2011) suggested that marsh vegetation will recover naturally under most conditions, at a rate depending on the degree of oiling, the amount of oil penetrating the soil profile, and the composition of plant species.

An early concern after the onset of the DWH blowout was the potential for harm to fish and fisheries (Jackson, 2010; Sumaila et al., 2012). The condition of oceanic red snapper became controversial soon after the onset of DWH as popular media reported that local fishermen caught fish with unusual fin lesions and skin ulcers. The lesions were suggested to be signals of a compromised immune system caused by exposure to toxic contaminants from the oil spill, although no peer-reviewed work on this subject existed at that time (Arias et al., 2013). Murawski et al. (2014) were cited frequently in the press for presenting "proof" of this exposure-effect link, but what Murawski et al. actually stated was that although they could not definitively link the cause (contaminants from the DWH spill) with the effect (increased prevalence of skin lesions) with only two years of post-event data, and neither could they reject the null hypothesis that lesion frequencies and PAH exposures were not linked. No link was actually proven and no other ecotoxicological literature suggests that this link exists.

Research in response to the DWH spill has made major advances in the understanding of the mechanisms of fish embryo toxicity and provided important evidence of the effects of oil toxicity on the fitness of surviving juvenile fish. Embryonic exposures to DWH oil caused a suite of developmental defects and cardiotoxicity characteristic of PAH toxicity in a variety of fish species. Field studies by Dubansky et al. (2013) found that embryos of Gulf killifish showed developmental abnormalities, including heart defects, delayed hatching and reduced hatching success after exposure to sediments from locations contaminated by the DWH oil spill. These findings mirrored the effects seen by de Soysa et al. (2012) who addressed oil toxicity to zebrafish in a laboratory study. Recently, the mechanisms of oil effects on cardiac morphology and physiology in fish embryos have been well-studied, not least by Incardona and colleagues in the NOAA Northwest Fisheries Science Center, Seattle, WA (Hatlen et al., 2010; Hicken et al., 2011; Incardona et al., 2014; Incardona et al., 2011; Incardona et al., 2013; Incardona et al., 2012a; Incardona et al., 2012b; Jung et al., 2013; Scott et al., 2011). The developing fish heart is a particularly vulnerable target for petrogenic 3- and 5-ringed un-substituted and alkyl-PAHs, which are primary constituents of crude and refined oils that are toxic to fish embryos, as shown by effects-driven chemical fractionation (Adams et al., 2014; Bornstein et al., 2014; Hodson et al., 2007) and structure-activity studies of individual alkyl-PAHs (Lin et al., 2015; Turcotte et al., 2011). Exposures of fish embryos and larvae to crude oil or refined oil, or to PAHs typical of oil, during sensitive windows of cardiac development induce an abnormal fluid accumulation in the pericardial space (pericardial edema) and inhibit or block potassium ion channels in heart muscle cells, causing an increased time for the heart to restart after every beat (Brette et al., 2014). These conditions impair the ability of the fish heart to pump blood and can lead to lethal heart failure. Cardiotoxicity is especially harmful to fast-swimming top predators such as Atlantic bluefin tuna, yellowfin tuna, and mahi-mahi, which are commercially- and ecologically-important fish species in the NGOM. Their migration, feeding, growth, survival, and reproduction depend on extremely efficient

circulatory systems. Interestingly, the study by Mager et al. (2014) demonstrated a significant reduction of swimming performance in mahi-mahi, which had been exposed to DWH oil as juveniles or embryos/larvae, suggesting negative implications for predator avoidance and prey capture behaviours and long-term survival and growth. Other developmental toxicities of Macondo type oil to fish have been demonstrated by Raimondo et al. (2014). The fish effect studies were discussed in the DWH litigation and the focus of the debate concerned the extent to which oil HC concentrations that induced these effects actually occurred. Further studies of the effect of oil exposure on cardiotoxicity and whole-animal performance in fish are expected soon, including studies with heart muscle cells of tuna. This research is highly relevant because the DWH oil spill coincided with the main spawning period for Atlantic bluefin tuna in NGOM, and this population contributes to high-value tuna fisheries from the Gulf to Nova Scotia, Canada. To understand the ecological implications of embryo toxicity, more research is needed to expand the array of fitness indicators in juvenile and adult fish, and to develop experimental and field research strategies to demonstrate the impacts of oil spills on fish abundance and trophic cascades.

Impacts of the DWH oil spill on other important seafood resources from the NGOM, such as oysters, shrimp and crabs, were less clear, e.g., as shown in several studies of oysters (Carmichael et al., 2012b; Moody et al., 2013; Soniat et al., 2011; Xia et al., 2012). In estuaries, mussels and other filter feeders such as barnacles, accumulated only minimal amounts of oil (Fry and Anderson, 2014), and bacteria associated with oysters were able to degrade the oil (Thomas et al., 2014). Observations of eyeless shrimp and clawless crabs were frequently reported in popular media as alarming evidence of impact to Gulf sea life caused by the DWH accident. However, to our knowledge, there is no research-based evidence for these field observations; or for possible effect mechanisms involved. Field mesocosm experiments with two shrimp species within Barataria Bay did find reduced growth of juvenile brown shrimps at heavily oiled locations, but not of white shrimp (Rozas et al., 2014). In contrast, shrimp were actually more abundant in areas heavily impacted by the DWH oil spill (van der Ham and de Mutsert, 2014). To explain the seemingly counterintuitive results, van der Ham and de Mutsert suggest that reduced fishing pressure due a closure of the shrimp fishery, or a delayed migration of adult shrimp to offshore spawning grounds (due to reduced growth in oil-affected shrimp populations) may have contributed to the observed increased abundance. Furthermore, shrimp catch statistics from the oil spill affected areas along the NGOM confirmed normal or increased catches compared to catch levels prior to 2010. For crabs, Felder et al. (2014) reported signs of declining diversity and abundance at deep waters and suggested an indirect effect of the DWH oil spill causing a loss of benthic seaweed cover in the affected areas. In coastal areas, there was significant toxicity of oil to two species of crab only at test concentrations greater than observed at sites contaminated by the spill (Anderson et al., 2014; Anderson Lively and McKenzie, 2014). In sum, the

available studies on NGOM crustaceans indicate a need for more research at the organism level to reveal cause-and-effect relationships of oiling stress in this organism group.

The unprecedented and large scale use of oil dispersants in the DWH response operation received much attention from the general public and the research community. More than 100 peer reviewed papers that concern some dispersant-relevant issue for DWH are now published. A considerable number of these studies addressed dispersant issues in coastal organisms and habitats, but these studies fall beyond the scope of the present review, as dispersants were not applied near coastlines during the DWH oil spill response. Dispersants were added to the jet of escaping oil at the wellhead as well as to offshore surface slicks; the former to generate and stabilize tiny, neutral buoyant oil droplets (<70 micrometer) to minimize vertical transport of oil to the surface, the latter to disperse floating oil into smaller oil droplets in the water column. From the studies reviewed here, there is an apparent consensus that the source dispersion contributed to an increased formation of large, deep, and neutrally-buoyant plumes of oily water that spread laterally from the Macondo site at a depth between 1000 and 1300 m in the NGOM (Socolofsky et al., 2015). Many studies report that the dispersants modified the spreading, dispersal, weathering, biodegradation, and toxicity of the spilled Macondo oil. A central question then is how the dispersant strategy influenced the total environmental impact of the DWH spill. As argued recently by Prince (2015), the potential environmental costs of adding dispersants to oil-polluted areas were likely outweighed by the oil having a shorter residence time, and hence a reduced integrated environmental impact. However, the novel source application of dispersants in the DWH response operation has been criticized. Some papers argue that the procedure created a deep-water spill with many new unknowns (Peterson et al., 2012), and that availability of environmental effects information for oil dispersant agents is limited and knowledge concerning individual components of dispersant products are largely proprietary (Berninger et al., 2011). It is likely that the way dispersants were used during the DWH response will have implications for future oil spill preparedness and oil spill response situations, in particularly for blowout situations at great depths. However, the use of dispersants in oil spill response is likely to remain controversial, judging from the intense disagreements between those who are in favor and those who are against dispersant use. Based on the DWH research studies conducted to date, the science community has not yet reached a general consensus about the appropriate role, if any, of dispersants in oil spill response. Hence, decisions on dispersant use will be site- and situation-specific, and depend on what marine and coastal ecosystem components and ecological resources are to be protected.

4. Summary and conclusion

The DWH oil spill incident in 2010 constituted an ecosystem-level injury in the NGOM. The spill resulted in an oil slick ultimately covering more than 112,000 km^2 on the ocean's surface. Oceanic currents, winds,

and wave action pushed the oil towards the coast, leading to various degrees of oiling along 2,100 km of shoreline in five US states, but most in LA, MI and AL. Fate-oriented studies show that oil spread both in deep waters (1100-1300 m depth) and at the surface. Only a minor part of the released oil (less than 15%, and possibly as little as 4%) made landfall along the coast; this partly due to the great depth of the blowout, the extensive use of oil dispersing agents (both at wellhead and surface) and other response measures (e.g., *in situ* burning), the massive bloom of oil degrading microbes, high surface water temperature and ocean currents. Effects-oriented studies demonstrated that the oil was toxic to a wide range of organisms; including plankton, invertebrates, fish, birds, and sea mammals, causing a wide array of adverse effects such as reduced growth, disease, impaired reproduction, impaired physiological health, and mortality. Oil concentrations exceeding threshold of toxicity occurred in surface waters, sediments, and marsh habitats in many locations, although the extent and degree of oiling varied greatly by time and location. The use of oil dispersing agents in offshore waters enhanced the bacterial degradation of oil, but also increased the bioavailability (and hence ecotoxicity impact) of the oil in certain offshore habitats. Both oil exposure and spill response actions caused injuries to a wide range of habitats, species and ecological functions over a vast area; although the situation has improved substantially from 2010 to the present. Ecological resources in the NGOM that were particularly impacted by DWH oil include deep ocean-bottom habitats and deep-sea corals, salt marsh ecosystems, organisms living at and in shoreline sediments and beach sand habitats, nearshore fish, shorebirds, floating *Sargassum* habitats and nearshore seagrass areas, sea turtles, dolphins and other cetaceans. Although there are numerous knowledge gaps and research needs still remaining, as highlighted throughout this review, the broad collection of environmental research conducted after DWH contributes significantly to our understanding of ecological impacts of major marine oil spills, and this learning helps to clarify which measures are needed, both pre-spill and post-spill, to reduce the environmental effects of such events.

Legend to figures:

Figure 1: The cumulative environmental footprint of the DWH oil spill in NGOM. Most surface slicks traveled toward shore, intersecting at least 2,100 kilometers of shoreline; and some slicks followed currents to the southeast. A deep-sea plume migrated more than 400 kilometers southwest of the wellhead. More than 400 flights dropped chemical dispersant on surface slicks, and more than 400 fires were set to burn off surface oil. Map source: DWH-NRDA (2015).

Figure 2: Fate scenarios for how oil released in a deep blowout situation behaves differently depending on application of oil dispersant. In the escaping jet at the wellhead, oil droplets of multiple sizes form and droplets above a certain size will rise toward the ocean surface. Adding dispersants stabilizes small oil droplets, thereby decreasing vertical oil transport. Illustration courtesy: Jack Cook, Woods Hole Oceanographic Institution.

Figure 3: Biological effects of the DWH oil spill. This conceptual figure illustrates the constellation of relationships between oil exposure and toxicological effects in organisms affected by the DWH oil spill. All exposure and effect elements shown in this figure are supported by information in the DWH oil spill research literature. Illustration adapted and extended from DWH-NRDA (2015).

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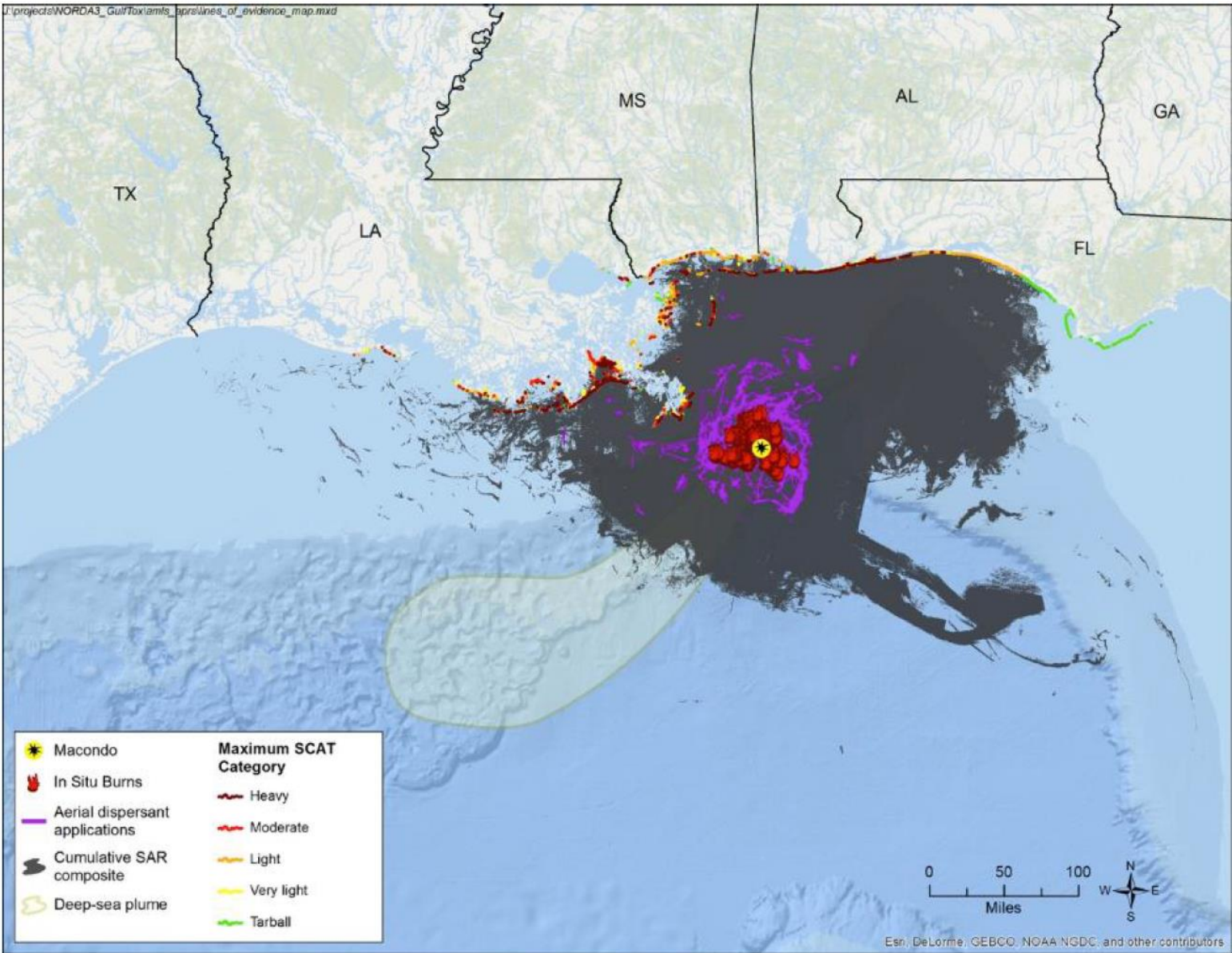
Figure 1

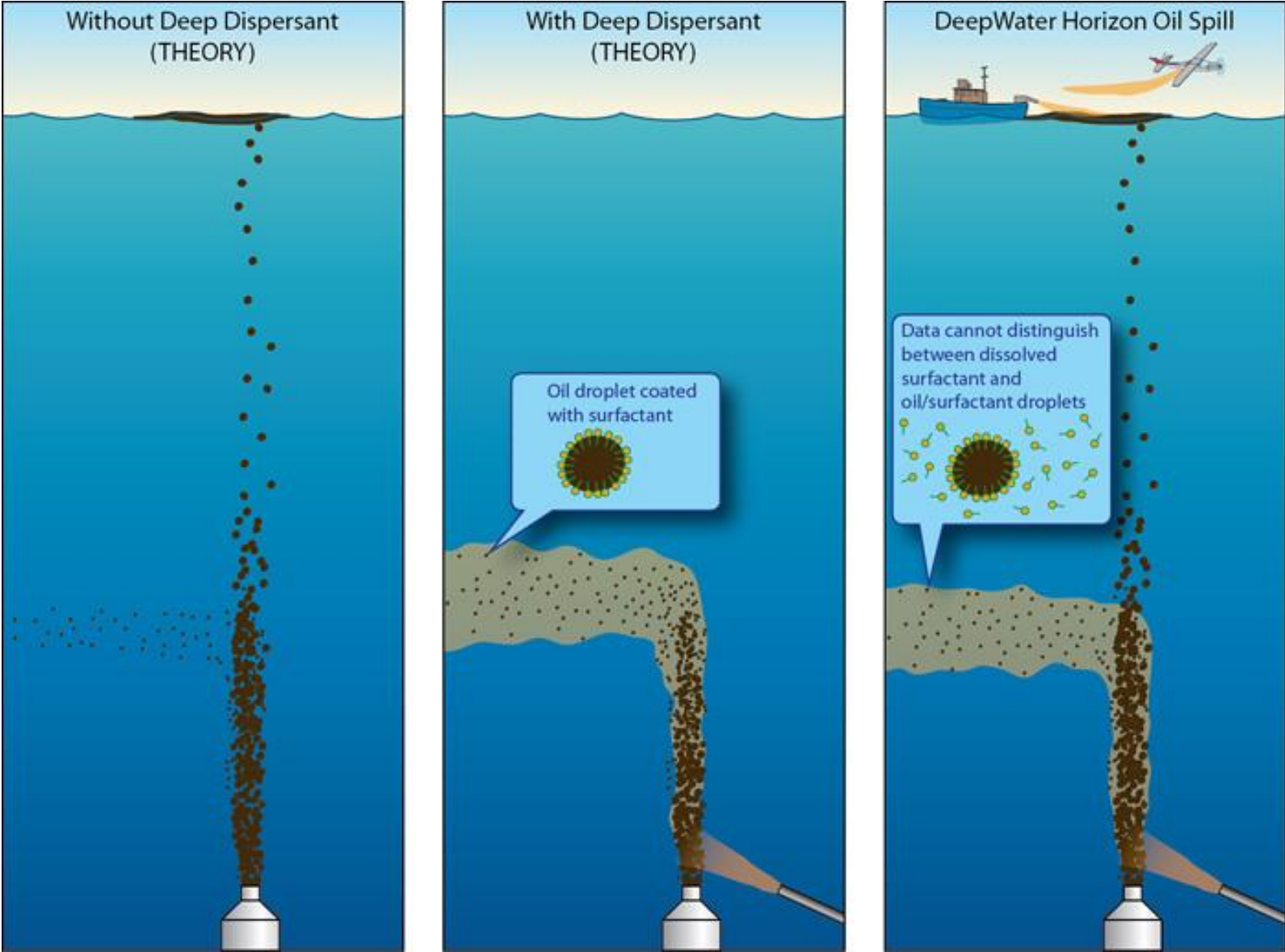Environmental effects of the Deepwater Horizon oil spill

Figure 2
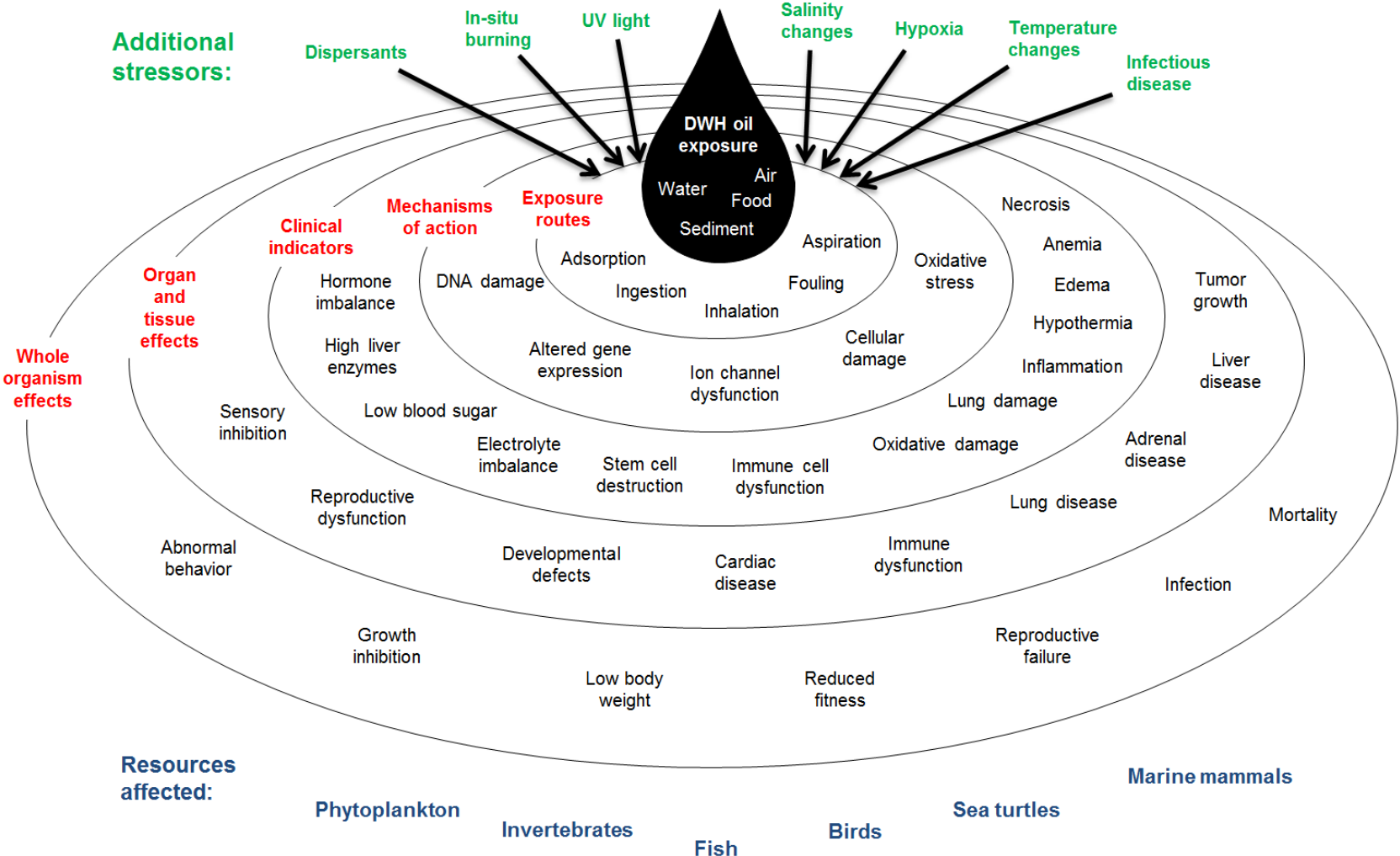
Environmental effects of the Deepwater Horizon oil spill

Figure 3