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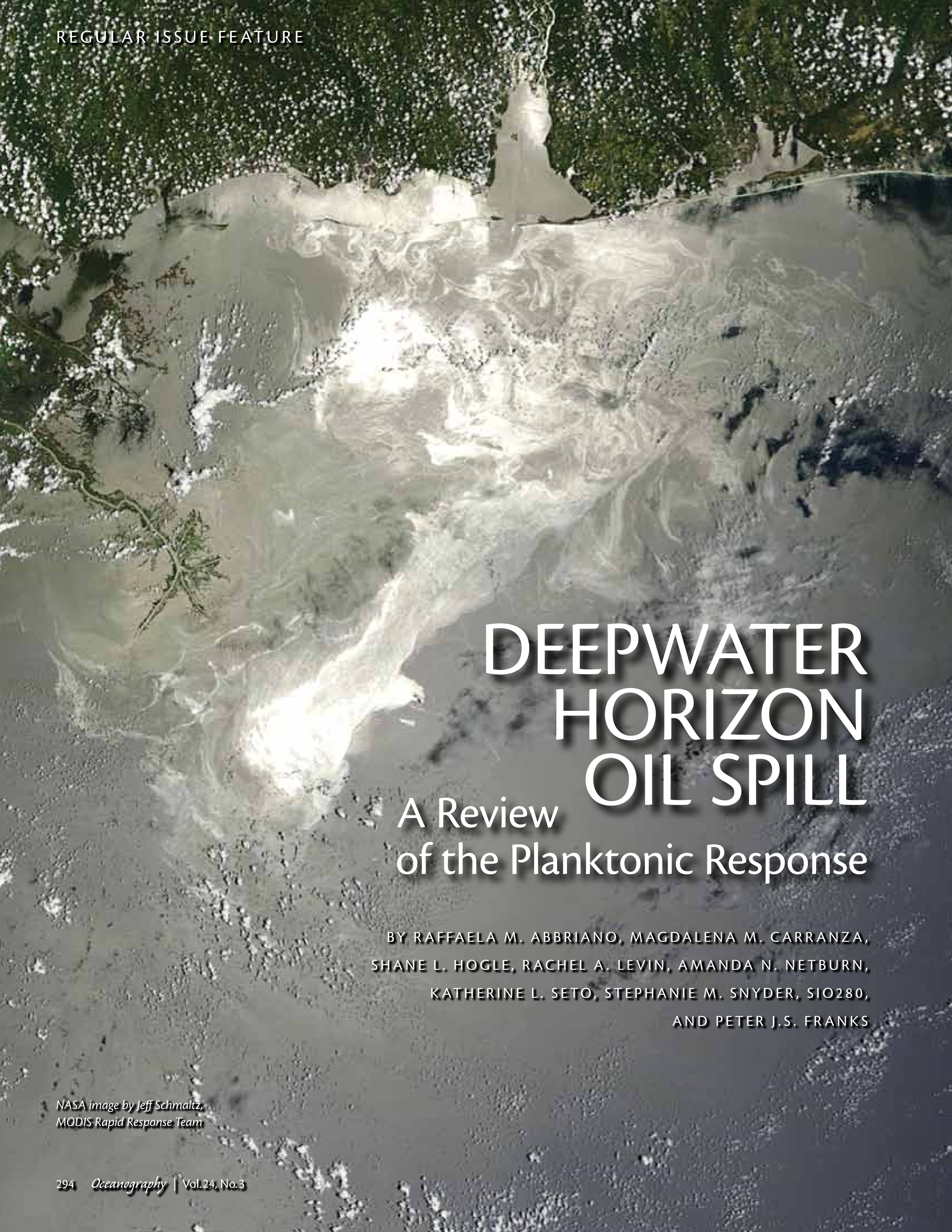

NASA image by Jeff Schmaltz, MODIS Rapid Response Team

DEEPWATER HORIZON OIL SPILL

A Review of the Planktonic Response

BY RAFFAELA M. ABBRIANO, MAGDALENA M. CARRANZA, SHANE L. HOGLE, RACHEL A. LEVIN, AMANDA N. NETBURN, KATHERINE L. SETO, STEPHANIE M. SNYDER, SIO280, AND PETER J.S. FRANKS

INTRODUCTION

On April 20, 2010, the explosion of the Deepwater Horizon (DWH) oil rig resulted in the loss of 11 lives and the largest oil spill in US history (Graham et al., 2010) and perhaps the second largest in the world, after the first Gulf War Oil Spill from Kuwait. Over the 84 days following the explosion, an estimated 6.7 x 10^5 mT of Louisiana Sweet Crude oil (United States Government, 2011) and up to 500,000 mT of methane and gases (Joye et al., 2011) were released from 1,480 m below the ocean's surface into the Gulf of Mexico (GoM). As oil continued to escape from the seafloor throughout the summer of 2010, images of oiled wildlife pervaded the news. These pictures, though troubling, only hinted at the fate of the plankton that form the foundation of the GoM ecosystem. This review discusses the potential effects of the DWH oil spill on the overlooked, but extremely important, members of the GoM ecosystem—the plankton. Our assessment is based on data collected in the aftermath of the DWH spill and supplemented with studies from past oil spills when information on the GoM spill was limited or unavailable. The time line we develop traces the spill from a "planktonic perspective," emphasizing the population dynamics of marine bacteria, phytoplankton, zooplankton, and fish larvae.

ECONOMICS AND ECOSYSTEM OF THE GULF OF MEXICO

With its white sandy beaches and productive waters, the GoM sustains a number of lucrative industries, including shrimp, oysters, menhaden, and bluefin tuna. The GoM shrimp fishery was valued at $367 million dollars in 2008 (NOAA, 2010). The larval stages of shrimp and other organisms are particularly vulnerable in oil-contaminated waters. Revenue losses from fisheries in Louisiana alone are estimated to be between $100–200 million (IEM, 2010). Tourism brings in an estimated $20 billion to the Gulf region (EPA, 2011), and huge losses are expected in the foreseeable future due to avoidance of areas impacted by the Deepwater Horizon disaster.

From April through June, the GoM serves as the sole breeding ground for western Atlantic bluefin tuna, a commercially important and endangered species. Atlantic bluefin tuna exhibit broadcast spawning in the oligotrophic waters of the GOM lower continental slope, including the area of surface oil dispersal (Figure 1; Teo et al., 2007; Muhling et al., 2010). They are the highest valued Atlantic tuna species in the Asian sushi and sashimi markets ($400 a pound at Tokyo's Tsukiji fish market), and they are overfished.

The GoM is also one of the United States' main sources of oil, with ~ 4,000 oil platforms that collectively produce almost a quarter of America's petroleum (Considine et al., 2004; Trevors and Saier, 2010). Up to 350 naturally occurring seeps distributed throughout the Gulf (Kvenvolden and Cooper, 2003) support microbial assemblages with a well-developed ability to oxidize hydrocarbons (Hazen et al., 2010). Respiration by these oil-degrading bacteria can create thin oxygen-minimum layers close to the seafloor (Bender et al., 2005), potentially affecting the communities that can live in those environments. However, GoM waters are well ventilated, and benthic oil-derived hypoxia tends to be local and transient (Bender et al., 2005).

> “WHILE STUDIES OF THE DWH OIL SPILL WILL CONTINUE TO PROVIDE NEW INFORMATION IN THE COMING MONTHS AND YEARS, EARLY RESEARCH SHOWS THAT THE PLANKTONIC COMMUNITY EXHIBITS AN ENCOURAGING LEVEL OF RESILIENCE.”

APRIL 20, 2010

The DWH oil platform explodes and sinks 66 km off the coast of Louisiana, allowing oil to escape uncontrolled from the Macondo wellhead.

Immediately following the explosion of the DWH oil rig, surface slicks of Louisiana Sweet Crude oil

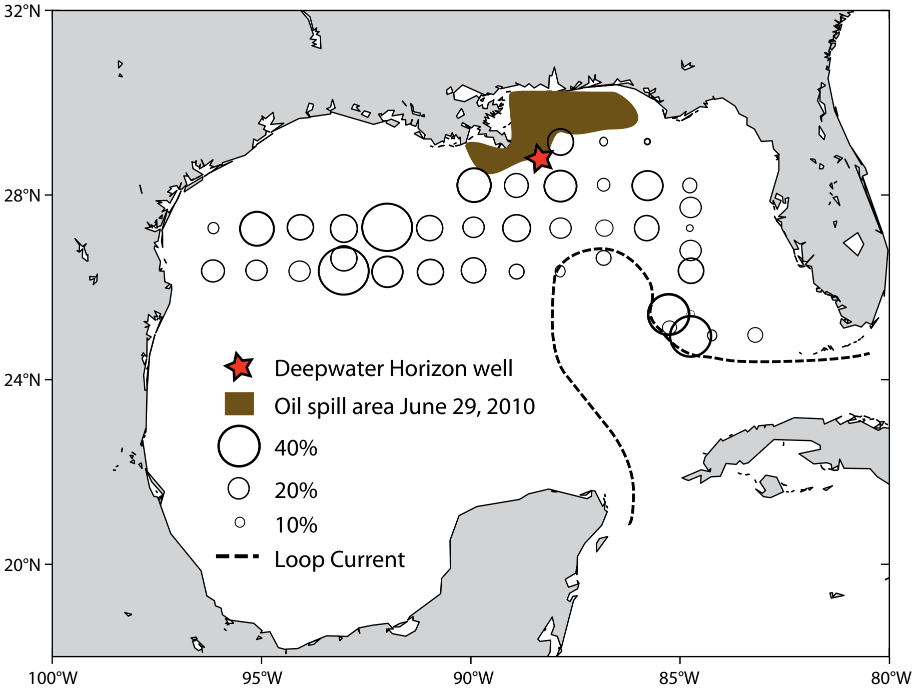

Figure 1. Map of the Gulf of Mexico showing the oil spill area as of June 29, 2010 (shading). Black circles show the probability of collecting at least one Atlantic bluefin tuna larva at sampling stations between 1982 and 2006. Black dashed line shows approximate location of the Loop Current. *Adapted from Muhling et al. (2010)*

began appearing, covering as much as 75,000 km^2 within one month (Cleveland et al., 2011). This crude oil is a structurally complex, heterogeneous mixture comprised of simple aliphatic hydrocarbons (SAHs), aromatic hydrocarbons (including polycyclic aromatic hydrocarbons, PAHs), resins, and asphaltenes. While dissolution—the chemical stabilization of crude oil components in seawater—is a minor pathway for oil loss compared with evaporation and emulsification, the dissolved fraction of crude oil is most toxic to aquatic species. This water-soluble fraction (WSF) tends to be comprised of low-molecular-weight aliphatic compounds, aromatic hydrocarbons, and PAHs. All oil types and grades contain WSFs of varying concentrations, but degraded crude varieties tend to have higher concentrations (National Research Council, 2003; Head et al., 2006). WSF components were detected at the DWH blowout with greatest signal intensities near 1,000 and 400 m depth. Although absolute concentrations could not be measured in the water column, it is likely that some portion of the total WSF migrated into the euphotic zone after the DWH spill (Camilli et al., 2010).

The chemical diversity of crude oil creates niches for bacterial substrate specialists during the course of biodegradation. Through the activities of various specialist bacteria, the composition and concentration of the chemical components of raw crude oil change over time (Dutta and Harayama, 2000; Head et al., 2006). A boom-and-bust cycle of bacterial succession is common, though not certain, after oiling events. A general community progression beginning with consumers of SAHs, followed by the consumers of PAHs and methane (Figure 2), frequently arises after marine oil spills, although this hierarchy can be altered or arrested depending on environmental conditions such as temperature, nutrient concentrations, salinity, and pressure (National Research Council, 2003; Valentine et al., 2010).

While the oil may have been a boon for certain bacterial types, both the oil and oil biodegradation can cause problems for phytoplankton in the immediate vicinity of a spill. Thick, buoyant oil slicks inhibit air-sea gas exchange and light penetration, both essential to photosynthesis and phytoplankton growth (González et al., 2009). The PAHs in the oil also affect phytoplankton growth, with responses ranging from stimulation at low concentrations of oil (1 mg L^{-1}) to inhibition at higher concentrations (100 mg L^{-1}; Harrison et al., 1986).

Like the phytoplankton, many zooplankton species are sensitive to the chemicals found in the oil. Copepods in direct contact with the spill were likely to experience increased mortality and decreased feeding and reproduction (Suchanek, 1993), potentially allowing blooms of phytoplankton (Figure 2). Tolerance to oil varies by species, and a study of GoM zooplankton communities

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found that mortality tended to be more dependent upon exposure time than concentration of oil (Figure 3), though the highest oil concentrations led to the highest mortalities (50% after 50 hours; Lee and Nicol, 1977). Copepods may also be able to sense and avoid oiled areas (Seuront, 2010), thus reducing their contact and potential mortality (Figure 4).

The same may not be true of Atlantic bluefin tuna larvae. PAHs are known to be highly toxic to larval herring, topsmelt, minnow, and salmon (Petersen and Kristensen, 1998; Heintz et al., 1999; Couillard et al., 2005). Toxic effects include hemorrhages, spinal deformities, growth retardation, and death (Billiard et al., 1999; Carls et al., 1999). While larvae of different fish species exhibit variable sensitivities to PAHs, deformities and/or death are probable for larvae that come into direct contact with the oil.

MAY 15–JULY 12, 2010

Of the estimated 2.1 million gallons of chemical dispersant (Corexit 9500 and Corexit 9527) released, more than one-third was injected at the wellhead site at depths greater than 1.5 km (Kujawinski et al., 2011).

The use of subsurface dispersants combined with high pressure and turbulence at the wellhead likely contributed to the formation of the subsurface oil plumes that were unique to the DWH (Kujawinski et al., 2011). Oil dispersants contain both surfactants and solvents, which lower interfacial tension between oil and water boundaries and reduce the tendency of oil to aggregate (Singer et al., 1994). The concentration of dissolved hydrocarbons increases by up to five times when Corexit is applied to crude oil (Fucik et al., 1994). Use of dispersant can expedite the removal of oil from the water column by increasing the rate of biodegradation by bacteria (Venosa and Holder, 2007). However, the literature is inconclusive as to the toxicological effects of dispersant on bacteria, with studies showing both growth enhancement and retardation (Mulkins-Philips and Stewart, 1974; Bruheim et al., 1999; Garcia et al., 2001). Still, key investigations have cautiously concluded that chemical dispersants are appropriate for enhancing microbial degradation (National Research Council, 2005). By late May, SAH-degrading bacteria, particularly the order *Oceanospirillales* (Hazen et al., 2010) had increased to the point that they represented over 90% of the bacteria inside the plume compared to only 5% in samples acquired outside the plume (Figure 2). Following the bloom of *Oceanospirillales*, another γ-proteobacteria from the genus *Cycloclasticus* known to degrade SAHs and PAHs bloomed in late June

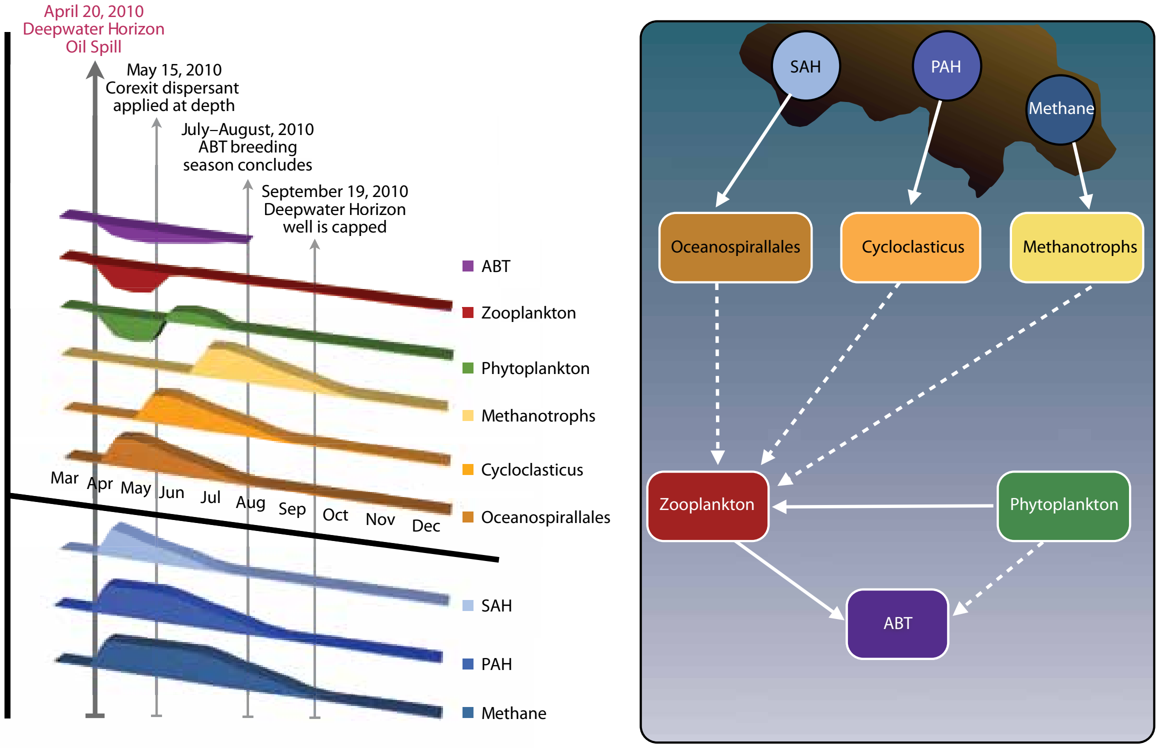

Figure 2. (left panel) Hypothesized (based on previous studies) time lines of oil-spill-driven changes in oil constituents (three lower time lines) and plankton. Vertical arrows indicate times discussed in the text. (right panel) Schematic food web indicating the oil constituents and their pathways into the planktonic food web. Colors correspond to the left panel.

(Kasai et al., 2002; Valentine et al., 2010). Respiration rates due to the degradation of SAHs were measured to be ~ 1 μM O_2 d^{-1} (Camilli et al. 2010), accounting for ~ 70% of the low-oxygen anomaly associated with the main plume (Valentine et al., 2010). Models of oxygen depletion due to bacterial respiration predicted hypoxia would occur within a few hundred kilometer radius of the wellhead at depths greater than 1,000 m (Adcroft et al., 2010). Though measurements showed oxygen drawdown, there was no evidence of hypoxia (Kessler et al., 2011).

Biodegradation by bacteria can also incorporate chemically dispersed oil into the food web. Graham et al. (2010) showed a decrease in the $\delta^{13}C$ of the small suspended particles (including phytoplankton) and mesozooplankton after the spill toward the $\delta^{13}C$ value of the local crude oil. This decrease implies uptake and transfer of components of the oil through the planktonic food web. Bioaccumulation of hydrocarbons at the base of the food web could increase exposure of higher-trophic-level organisms, with potentially delayed negative effects (Wolfe et al., 1998).

The mixture of crude oil and Corexit has been found to be more toxic to phytoplankton and fish larvae than oil alone (Hsiao et al., 1978: a mixture of four different oils; Middaugh and Whiting, 1995: WSF of No. 2 Fuel Oil). Acute toxicity tests on the larval stages of several invertebrates indigenous to the GoM, such as shrimp, oysters, and crabs, showed that mixtures of the GoM oil from different wells and Corexit were about as toxic as the WSF of the oil alone (Fucik et al., 1994). Most of the toxicity of the oil-Corexit mixture occurred in the first 24 hours, probably due to the increased volatilization of certain components of the oil (Fucik et al., 1994). In some experiments, increases in toxicity could be attributed to the chemical properties of dispersants, which can affect the cellular membranes of planktonic organisms by increasing permeability to toxic chemicals, disrupting respiration, and causing membrane lysis (Singer et al., 1991).

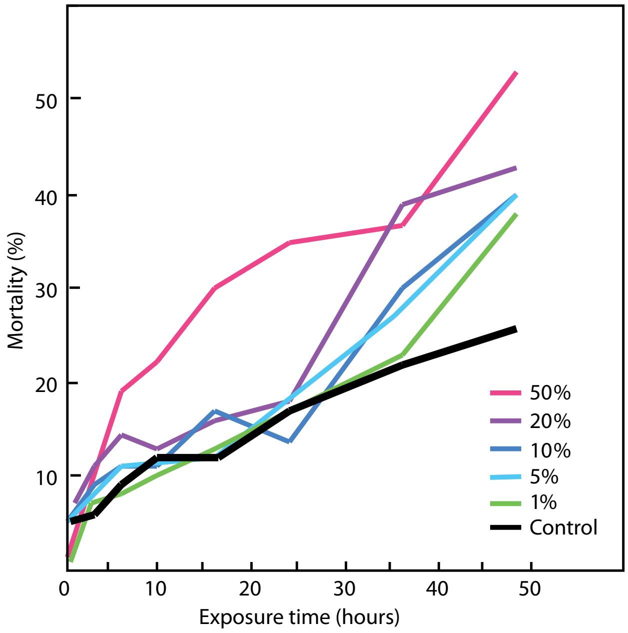

Figure 3. Mortality of a mixture of coastal zooplankton exposed to the water-soluble fraction (WSF) of No. 2 fuel oil at various concentrations. Note that mortality depends primarily upon exposure time rather than on concentration, though the highest concentrations lead to the highest mortality after 50 h. *From data in Lee and Nicol (1977)*

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After three months, the DWH well was finally capped. Relief wells were drilled, and the wellhead was declared effectively dead.

At the time of the well capping, studies were beginning to reveal a resilient GoM planktonic ecosystem, reflecting a local adaptation to natural oil seeps. Changes in the structure of bacterial communities were seen mainly in the relatively short-term shifts in dominance from *Oceanospirillales* (SAH degraders) to *Cycloclasticus* (PAH degraders) (Figure 2). Subsequently, almost all of the released methane from the spill was eliminated by a bloom of bacterial methanotrophs in late August that oxidized CH_4 to CO_2 (Kessler et al., 2011). Although this rapid oxidation of methane raised concern about the potential for hypoxia, measurements by Kessler et al. (2011) showed that dissolved O_2 concentrations—while low—were about three times higher than the level at which fisheries would be threatened (Camilli et al., 2010).

Meanwhile, we speculate that phytoplankton community structure changed and biomass increased (Teal and Howarth, 1984) due to a combination of the detrimental effects of oil contamination and the beneficial effects of decreased predation. Similarly, a predicted rapid recovery of the zooplankton would be due to their short generation times and high fecundity, their ability to avoid oily patches (Seuront, 2010), and their recruitment from unaffected areas. In most historical oil spills, zooplankton abundance and community structure did not appear to be affected beyond several weeks following the incident (Davenport, 1982; Johansson et al., 1980; Varela et al., 2006). Therefore, we hypothesize that any initial phytoplankton increase or zooplankton population decline would be transient (Figure 2).

Hydrocarbon-degrading microbes provided a link between the plumes of oil generated at depth and the rest of the oceanic food web. Graham et al.'s (2010) study demonstrated that both the mesozooplankton and small particulate matter had incorporated oil-derived (low δ^{13}C) carbon; the overall impact of this transfer to zooplankton is yet to be determined. However, sampling in the area showed that recovery to pre-spill δ^{13}C values only took about two to four weeks (Graham et al., 2010).

As the oil makes its way up the food chain, its effects on Atlantic bluefin tuna larvae remain unclear. While contact with the oil probably resulted in larval mutation or death, the boom-and-bust cycles in the microbial loop may have led to increases in the main prey sources of these larvae, namely heterotrophic microplankton (Llopiz et al., 2010; Nakagawa et al., 2007). Therefore, for the Atlantic bluefin tuna, being in the right place at the right time may prove to be the deciding factor for the population.

CONCLUSION

While studies of the DWH oil spill will continue to provide new information in the coming months and years, early research shows that the planktonic community exhibits an encouraging level of resilience. Its pre-existing acclimation to the presence of hydrocarbons, as well as its diversity and specialization, may have predisposed the community to respond to and even exploit a seemingly catastrophic event such as the DWH oil spill. Specialists within the diverse bacterial communities exhibited rapid boom-and-bust cycles, showing signs of returning to background levels as early as 60 days after the blowout. Although individual phytoplankton species may have experienced relative mortality or enhanced growth, the direct negative effects of oil were probably largely offset by a decrease in predation. Dispersion and degradation of oil in surface seawater, high rates of reproduction of marine planktonic organisms, and circulation and mixing in the ocean may also have contributed to rapid recovery of phytoplankton populations within weeks to months. Zooplankton, due to rapid reproduction and ability to avoid direct contact with oil, may have been minimally affected in the long run. Lastly, Atlantic bluefin tuna would likely suffer significant mortality with direct oil contact, but secondary effects such as an increase in food supply are still to be determined. Therefore, while delayed impacts of bioaccumulation in higher trophic levels may still prove significant, the direct impacts of DWH oil on the planktonic community—marine bacteria, phytoplankton, zooplankton, and fish larvae—provide some hope for a resilient and thriving GoM.

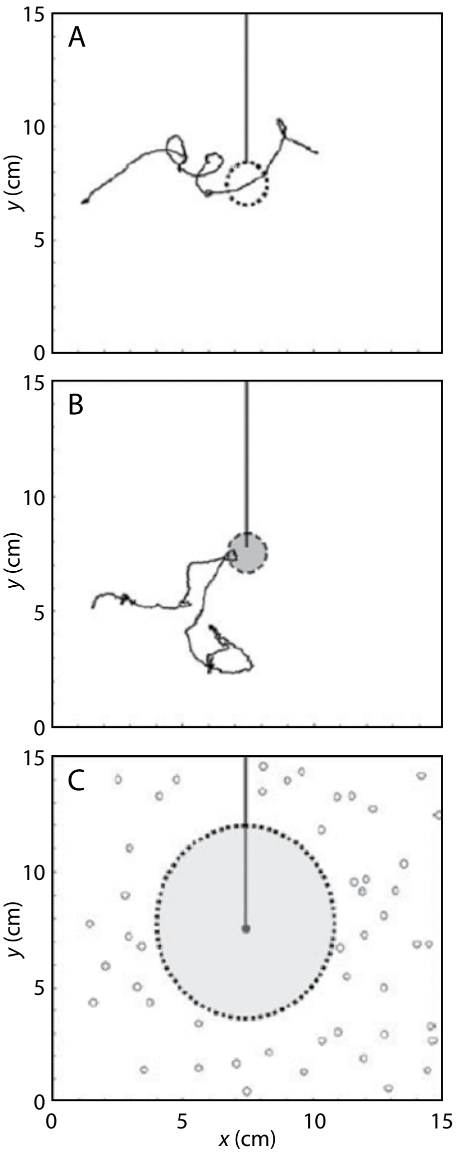

Figure 4. (A) Movement of a copepod around an uncontaminated sample (open circle). (B) Movement of a copepod around a patch containing the water-soluble fraction of diesel oil, showing patch-avoidance response. (C) Distribution of copepods around a patch of the water-soluble fraction of diesel oil, showing that they avoid entering the patch. *Adapted from Seuront (2010)*

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