How Were Phytoplankton Affected by the *Deepwater Horizon* Oil Spill?

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*A literature review demonstrates that crude oil spills can affect phytoplankton, favoring the growth of some while inhibiting the growth of others. Subsequently, the phytoplankton assemblage can change as a result of exposure to crude oil. Studies of phytoplankton responses to the Macondo (*Deepwater Horizon*) oil spill indicate that the phytoplankton may have been stimulated by the oil spill, although the presence of low-salinity water in the region makes it difficult to discount the importance of riverine-borne nutrients as a factor. A few studies suggest that the oil spill was toxic to some phytoplankton species, whereas others indicate that the degree of tolerance to the oil or to dispersants differs among species. These results generally comply with findings of previous studies, but a lack of published field data analyses prevents further assessment of the impacts of the* Deepwater Horizon *oil spill on phytoplankton population dynamics in the northern Gulf of Mexico.*

Keywords: Macondo, petroleum, PAH, hydrocarbon, algae

The impact of crude oil on marine organisms has been studied extensively; however, organisms at higher trophic levels have garnered more attention than have those at the base of the marine food web, such as phytoplankton. Phytoplankton play a key role in the ecology of the marine ecosystem, and they are also an integral part in the regulation of the amount of carbon in the atmosphere; therefore, changes in their patterns of distribution and abundance can have a significant impact on the entire ecosystem. Some studies have demonstrated that crude oil can alter water conditions (e.g., chemical composition, food web interactions) to enhance phytoplankton growth and increase their biomass (e.g., Lee et al. 1977, Elmgren et al. 1980, Ozhan et al. 2014). However, some phytoplankton groups can play an active role in altering crude oil compounds in conjunction with microbial communities (McGenity et al. 2012). The impact of crude oil is not limited to phytoplankton in the water column; microphytobenthos are also affected by hydrocarbon exposures (Riaux-Gobin 1985). Settling of a relatively heavier fraction of oil can change benthic food web interactions (Carman et al. 1997) and can enhance microalgal biomass (Carman et al. 1995).

In many of the previous studies, responses both in single phytoplankton species and community structures of phytoplankton were assessed. However, less attention has been paid to potential impacts on phytoplankton species at the cellular level and to the modes of action of crude oil hydrocarbons. In this review, we attempt to examine recent literature on phytoplankton responses to crude-oil-related pollution in marine systems, with a focus on the impact of the Macondo blowout in the Gulf of Mexico (GOM). The discussions featured herein cover the historical data on the impact of crude oil on phytoplankton, potential implications of the Macondo blowout based on current studies and on predictions of crude oil toxicities from previous literature, and prospective problems related to the assessment of crude oil toxicity in the phytoplankton community.

Assessment of historical data

The various phytoplankton groups encompass a wide range of physiologies, resulting in a multitude of responses and tolerances to oil toxicants (Harrison 1986, Meng et al. 2007, Wang et al. 2008). Other influential factors include the geographic location, oceanographic and meteorological conditions, seasonal variations, oil dosage and impact area, and oil type (NRC 2003). In addition to the direct toxic effects of crude oil and its components on phytoplankton cells, crude oil has some other effects that can also be detrimental. One example is the formation of oil films (or slicks) on the water surface, which can limit gas exchange through the air–sea interface and can reduce light penetration into the water column by up to 90% (Nelson-Smith 1973), limiting phytoplankton photosynthesis (González et al. 2009).

Although the factors that govern the toxicity of crude oil to phytoplankton are not well understood, the properties of the receiving water body seem to play a role. Temperature is one such factor. Huang and colleagues (2011) demonstrated that the diatom *Skeletonema costatum* had a high tolerance to the water-accommodated fraction (WAF) of crude oil in winter; however, during the summer, even low WAF

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concentrations limited growth. The researchers suggested that an increase in temperature caused an increase in metabolic rate, leading to greater body absorption of toxicants and, therefore, to further toxicity. In a study by Østgaard and colleagues (1984), *S. costatum* had a low tolerance to crude oil in a cold-water environment; conversely, the same species was shown to be very tolerant in temperate waters in a study by Vargo and colleagues (1982). The geographic origin of phytoplankton (i.e., oceanic or coastal species) also appears to play a role. For example, microcosm experiments conducted by Gonzáles and colleagues (2009) demonstrated that crude oil negatively affected oceanic phytoplankton relative to coastal phytoplankton assemblages. In addition, nutrient concentrations affect the sensitivity of phytoplankton to oil toxicity. Ozhan and Bargu (2014a) showed that differences in phytoplankton community composition changes were due to crude oil exposure under nutrient-rich and nutrient-deficient conditions. A nutrient-rich environment lessened the inhibitory effects of the crude oil on phytoplankton relative to a nutrient-deficient environment. In another study, phosphorus-deficient cultures of *S. costatum* displayed a higher sensitivity to hydrocarbons than did nitrogen- or silica-deficient cultures (Karydis 1981).

Crude oil contains many different compounds, each of which may cause distinct harm to phytoplankton. Laboratory-based toxicity studies on phytoplankton have been conducted to determine the mode of action of crude oil. For example, a gene expression study (Hook and Osborn 2012) demonstrated that crude oil, dispersed oil, and the dispersant have similar modes of action on phytoplankton (cell membrane genes were commonly affected in all three treatments). This study verified the results of an earlier study, which demonstrated that lipophilic oil compounds accumulate in the cell membrane and change its structural and functional properties, including the loss of cell permeability and other types of irreversible damage at the cell surface (Sikkema et al. 1995). Crude oil has also been shown to cause morphological changes (Tukaj et al. 1998), reduced cell nuclei (Tukaj et al. 1998), and the loss of cell mobility (Soto et al. 1975). Crude oil interferes with photosynthetic processes and decreases total primary production in phytoplankton (e.g., Miller et al. 1978, Karydis 1981, Harrison et al. 1986, González et al. 2009). Other observational impacts included the shrinkage of chloroplasts (Smith JE 1968, Tukaj et al. 1998) and pyrenoids (Tukaj et al. 1998), the loss of other pigments (Smith JE 1968), and the loss of carbon dioxide (CO_2) absorption (Koshikawa et al. 2007). Crude oil exposure was also shown to cause an interference of nucleic acid synthesis (El-Sheekh et al. 2000), a reduction of protein content (Chen et al. 2008), and damage to (and alterations of) DNA and RNA (El-Sheekh et al. 2000, Parab et al. 2008). Cells exposed to hydrocarbons also exhibited oxidative stress (Tukaj and Aksmann 2007) and interference with antioxidant defense system operations (Wolfe et al. 1999).

Short-term negative effects on phytoplankton (such as growth inhibition) are usually observed in the presence of high concentrations of these toxigenic compounds. When phytoplankton mortality occurred at high crude oil concentrations, however, no correlation was found between toxicity and exposure time (Miller et al. 1978, Adekunle et al. 2010). In general, field and laboratory studies have shown that crude oil concentrations up to 1.0 milligram per liter (mg/L) may stimulate phytoplankton growth, concentrations between 1.0 and 100 mg/L may cause slight and severe growth inhibition, and concentrations over 100 mg/L result in severe or complete growth inhibition (references are given in tables 1, 2, and 3). The impact range of crude oil (half maximal effective concentration values) generally varied between 1 and 100 mg/L (table 1). Individual crude oil compounds generally had larger impacts than crude oil, with polycyclic aromatic hydrocarbons (PAHs) having the highest toxicity potential on phytoplankton at a level of 1 micrgram per liter (table 2).

In addition to the inhibition and stimulation of individual phytoplankton species grown in the presence of crude oil, community composition changes have been studied to better understand effects on the structure and function of the natural ecosystem (reviewed in table 3). Community responses are difficult to predict, because the responses will be based in part on the relative tolerances of the different phytoplankton groups present at the time the community was exposed to the crude oil (Gonz**á**les et al. 2013).

Both individual- and community-level studies have indicated that certain groups have a greater sensitivity to crude oil. For example, the suppression of diatom growth and the rise in dominance of flagellates have been observed following oil spills and in laboratory experiments (e.g., Lee et al. 1977, Elmgren et al. 1980, Harrison et al. 1986). Siron and colleagues (1991) stated that diatoms are more sensitive to crude oil because of the presence of their external silica frustule. This structure absorbs hydrocarbons very well, allowing these crude oil components to be retained, thereby enabling subsequent toxicity or hindering sexual reproduction and auxospore formation in the diatoms (Kustenko 1981). Diatom susceptibility to oil varies among species, however, allowing some species to thrive as others are inhibited (González et al. 2009, Adekunle et al. 2010, Gilde and Pinckney 2012, Ozhan et al. 2014). This observation raises a larger query: Does the relative tolerance of different phytoplankton groups depend on taxonomic classification, or are other factors involved? For example, cell size may play a role. Gonzáles and colleagues (2009) reported that small diatoms (smaller than 20 micrometers) were not only more tolerant to crude oil than were bigger diatoms, but their growth was stimulated under low concentrations of crude oil. Huang and colleagues (2011) reported that the relatively smaller phytoplankton *S. costatum* and *Melosira moniliformis* became the dominant species and showed greater tolerance to crude oil than did the larger phytoplankton *Ditylum brightwellii* and *Biddulphia mobiliensis*. According to Gonzáles and colleagues (2009), the reason for which smaller phytoplankton species may survive better than larger species might be

Table 1. Historical data of individual phytoplankton responses to crude oil.

Species	Crude oil	Response (EC_{50}, in milligrams per liter)	Duration	Reference
Monochrysis lutheri	Amoco Cadiz	4.4	2 hours	Vandermeulen et al. 1979
M. lutheri	Bunker C	3.3	2 hours	Vandermeulen et al. 1979
Phaeodactylum tricornutum	Arabian light	16.4	14 days	Siron et al. 1991
Dunaliella tertiolecta	Arabian light	36	14 days	Siron et al. 1991
Thalassionema frauenfeldii	Nigerian	>50	24 hours	Adekunle et al. 2010
Coscinodiscus centralis	Nigerian	>50	24 hours	Adekunle et al. 2010
Ceratium trichoceros	Nigerian	>50	24 hours	Adekunle et al. 2010
Odontella mobiliensis	Nigerian	>50	24 hours	Adekunle et al. 2010
Chaetoceros socialis	South Louisiana	1.84	10 days	Ozhan et al. 2014
Ditylum brightwellii	South Louisiana	2.50	10 days	Ozhan et al. 2014
Heterocapsa triquetra	South Louisiana	1.03	10 days	Ozhan et al. 2014
Pyrocystis lunula	South Louisiana	1.75	10 days	Ozhan et al. 2014
Scrippsiella trochoidea	South Louisiana	1.14	10 days	Ozhan et al. 2014

Abbreviation: EC_{50}, half maximal effective concentration.

Table 2. Selected data of individual phytoplankton responses to crude oil compounds.

Species	Test substance	Response (EC_{50}, in micrograms per liter)	Duration (in days)	Reference
Phaeodactylum tricornutum	Anthracene	123	3	Wang et al. 2008
Skeletonema costatum	Anthracene	39	3	Meng et al. 2007
Thalassiosira pseudonana	Benzo(a)pyrene	55.2	3	Bopp and Lettieri 2007
Heterocapsa triquetra	Benzo(a)pyrene	7.02	10	Ozhan and Bargu 2014
T. pseudonana	Fluoranthene	1031	3	Bopp and Lettieri 2007
S. costatum	Fluoranthene	18	10	Meng et al. 2007
Ditylum brightwellii	Naphthalene	1.01	3	Ozhan and Bargu 2014b
S. costatum	Phenanthrene	47	3	Meng et al. 2007
P. tricornutum	Phenanthrene	154	3	Wang et al. 2008
P. tricornutum	Pyrene	119	3	Wang et al. 2008
T. pseudonana	Pyrene	260.3	3	Bopp and Lettieri 2007

Abbreviation: EC_{50}, half maximal effective concentration.

their indirect trophic interaction resulting from the release of predation on smaller species. Conversely, Sargian and colleagues (2007) observed that picophytoplankton were less tolerant of oil than nanophytoplankton were. They speculated that the lower tolerance of picophytoplankton was due to their smaller size and was associated with a larger surface area to volume ratio. Similarly, Echeveste and colleagues (2010) investigated cell-size-dependent toxicity thresholds of polycyclic aromatic hydrocarbons and found that larger phytoplankton cells were generally more tolerant of PAH exposure than were smaller cells.

Microbial degradation also plays a major role in the weathering process of crude oil and in consequent alterations of its toxicity to phytoplankton (Head et al. 2006). Biodegradation is a complex process in natural ecosystems; so far, 79 bacterial, 9 cyanobacterial, 103 fungal, and 14 algal genera are known to degrade or transform these hydrocarbons (Prince 2005). Because of close interactions between phytoplankton and microbial communities, it is hard to ignore the impact of biodegradation processes and microbial communities on phytoplankton at spill sites. In the case of crude oil biodegradation, the role of microorganisms—particularly bacteria in conjunction with microalgae—is highly complex and significant (for a review, see McGenity et al. 2012). Even though a solid mechanistic explanation of the relationship between hydrocarbon-degrading bacteria and phytoplankton has not yet been reported, it is known that a close relationship exists between them in the marine environment, particularly in the presence of hydrocarbons (McGenity et al. 2012). Although phytoplankton provides

Table 3. Phytoplankton community responses to crude oil.

Crude oil type	Concentration (in micrograms per liter)	Duration (in days)	Remarks	Reference
Prudhoe Bay	2000–4500	17	Shifting community from diatoms to microflagellates such as haptophytes, chrysophytes and a prasinophyte	Harrison et al. 1986
Bunker A	22	10	Suppression of diatoms, flagellates predominated	Nomura et al. 2007
Prestige oil	8.6–23[a]	5	Diatoms more resistant, larger diatoms affected more than smaller diatoms, oceanic phytoplankton more susceptible to crude oil exposure	González et al. 2009
South Louisiana and Texas	10–100	2	Diatoms, chlorophytes, and euglenophytes were resistant; prasinophytes not affected	Gilde and Pinckney 2012
Prestige oil	20–60[a]	8	Community dominated by diatoms, initial compositions of communities determined response	González et al. 2013
South Louisiana	270–520	10	Diatoms showed the greatest tolerance, nutrient regime affects community composition	Ozhan and Bargu 2014[a]

[a]Chrysene equivalents.

oxygen, dissolved and volatile organic matter, and extracellular polymeric substances to bacteria, they, in turn, can provide CO_2, exopolysaccharides, vitamins, nutrients, enzymes, and iron to phytoplankton (for a summary, see McGenity et al. 2012) by using hydrocarbons. This exchange could provide an advantage to phytoplankton cells that survived the acute toxic effects of oil—particularly phytoplankton in oligotrophic waters. The positive impact of high nutrient concentrations in crude-oil-contaminated water on crude oil toxicity to phytoplankton was recently reported by Ozhan and Bargu (2014a). Other studies have also shown enhanced degradation of hydrocarbons when bacteria and phytoplankton coexist (e.g., Warshawsky et al. 2007, Abed 2010) and confirm this close relationship.

This review of the literature reveals several aspects of how crude oil spills can affect phytoplankton communities. First of all, the interactions between crude oil components and phytoplankton are complex, varying among crude oil compounds, concentrations, and phytoplankton species. Second, other environmental factors play a role, including temperature, light, and the nutrient regime. Third, one can expect varying responses from the different members of the phytoplankton community; some taxa may be stimulated, whereas others may be hindered, or differences in sensitivity could cause a decrease in the biomass of all species at different levels, without a stimulation of any species. Grazers may be affected, which relieves grazing pressures on some phytoplankton species but not on others. Because of the significance of microbial degradation of crude oil, the close coupling between phototrophs and heterotrophs can also play a prominent role in the marine environment during and after oil spills. The resultant imbalances may result in phytoplankton assemblage shifts in response to the spill. We will examine this using the available data from the Macondo (*Deepwater Horizon* [DWH]) oil spill.

Impacts of the Macondo blowout on phytoplankton

The Macondo blowout was the largest accidental oil spill in US history, and the fate of this oil within the GOM ecosystem remains to be fully understood. Complex oceanographic processes have made it difficult to determine the current and future distribution of crude oil throughout the benthos and water column and its persistence in the marine environment (Smith RH et al. 2014). A study on the geographic extent of petroleum hydrocarbon distribution in sediment, seawater, biota, and seafood during and after the Macondo blowout showed that the spill extensively contaminated the coastal areas from Louisiana to Florida (Sammarco et al. 2013). Furthermore, evidence for exposure of the DWH oil spill to coastal phytoplankton communities was shown by carbon isotopes $\delta^{13}C$ (Graham et al. 2010) and $\Delta^{14}C$ (Chanton et al. 2012). Most important, there are no immediate answers to questions concerning the short-term and long-term impacts on phytoplankton communities in the path of this disaster. Although it is difficult to predict the impacts of an oil spill of this magnitude on the future of phytoplankton communities in the region, we can infer possible effects by assessing current studies. We will examine the available data in terms of stimulation, toxic effects, and assemblage shifts.

Remote sensing analyses suggest that the Macondo blowout stimulated phytoplankton growth. In August 2010, a large area (more than 11,000 square kilometers) in the northeastern GOM appeared to have very high concentrations of chlorophyll (according to the analysis of MODIS fluorescence line height [FLH] data; Hu et al. 2011). In fact, the FLH values were higher in August 2010 than during any

August since 2002, even when river discharges were higher. In addition, there was no significant river anomaly observed in summer 2010, and FLH anomalies did not correlate with river discharge anomalies over the course of the analyzed MODIS time series (2002–2009) in the region where the FLH patch occurred in August 2010. Rather, the high-FLH patch did coincide with oil locations inferred from satellite imagery and predicted by circulation models. These results suggest that phytoplankton were stimulated by the Macondo oil spill. There was also evidence of patchy phytoplankton blooms off of Southwest Pass (to the west of the Mississippi River's birdfoot delta), possibly because of stimulatory effects from the oil spill (Sonia C. Gallegos, Naval Research Laboratory, Stennis Space Center, Mississippi, personal communication, 4 April 2014), although riverine inputs cannot be discounted in this case. By 2011, however, the chlorophyll concentrations were typical of pre-oil spill conditions, which suggests that the impact of the oil spill on the phytoplankton was strong but short lived (Sonia C. Gallegos, personal communication, 4 April 2014).

The DWH oil spill may have also stimulated the production of marine snow in the region. Passow and colleagues (2012) studied possible causes for the large marine snow formation event observed in oil-contaminated surface waters of the GOM after the oil spill. Their experimental results indicated that the marine snow was formed by mucus produced by oil-degrading bacteria coupled with the coagulation of oil compounds and suspended particulate matter, as well as phytoplankton and oil droplets. Increased marine snow production could enhance the benthic flux of oil (and particulate organic matter) to the benthos, possibly influencing degradation processes and benthic hypoxia.

Although it is a known fact that microbial communities have adapted themselves to hydrocarbon exposures through their chronic release from natural hydrocarbon seeps within GOM coastal ecosystems, the Macondo blowout extensively increased the abundance, activity, and diversity of microbial communities, especially in the photic zone of the GOM (e.g., Edwards et al. 2010, Hazen et al. 2010, Ziervogel et al. 2012). Exopolysaccharides released from whole bacterial (Gutierrez et al. 2013) and possibly eukaryotic phytoplankton cells (Passow et al. 2012) increased the solubilization and biodegradation of aromatic hydrocarbons (Gutierrez et al. 2013). The resulting degradation products could be beneficial to phytoplankton growth; however, studies have yet to support this.

Although there is some evidence for a stimulatory effect of oil on phytoplankton from previous spills, a study conducted after the Macondo blowout indicated that diatom communities from Perdido Bay, Florida, were not negatively affected by the oil spill (Adhikari et al. 2012). The study showed that there was a larger number of taxa, a greater diversity of diatom species, and an insignificant number of deformed phytoplankton valves relative to historical data from prior to the oil spill. However, other studies indicate toxic impacts of the oil on the phytoplankton. For example, Paul and colleagues (2013) collected water samples from the northeastern GOM soon after the oil spill (August 2010) and found that 34% (4 of 13) of the samples were toxic to phytoplankton according to the QwikLite assay (a bioassay dependent on the bioluminescence of the dinoflagellate *Pyrocystis lunula*). Other toxicity tests (the Microtox and λ-Microscreen prophage induction assays) indicated that toxicity was correlated with total petroleum hydrocarbon concentrations. Although Hu and colleagues (2011) observed an increase in chlorophyll concentrations in August 2010, photosynthetic capacity was reduced in near-surface waters relative to those in later months, which suggests a possible negative impact on the phytoplankton (Paul et al. 2013).

Not all phytoplankton responded the same way to oil exposure, however. In a laboratory-based study, Ozhan and colleagues (2014) tested the toxicity of South Louisiana sweet crude (LSC) oil on five species of phytoplankton and found that dinoflagellates were more tolerant of oil exposure at lower concentrations (fewer than 1200 parts per billion), whereas diatoms where more tolerant at higher concentrations. Larger species were more tolerant overall than smaller species. In addition, each phytoplankton species showed considerably less tolerance to LSC oil in the presence of the other four phytoplankton species relative to their individual responses. This study also showed that addition of Corexit increased the toxicity of the crude oil considerably, and Corexit, itself, was toxic to phytoplankton species at very low levels.

Microcosm experiments were conducted on natural phytoplankton communities with Macondo oil and Corexit 9500A treatments (each alone and in combination) in addition to ultraviolet light exposure (to test for phytotoxicity). Dispersed oil (oil and Corexit) caused the largest decrease in chlorophyll-*a* concentrations but also caused an increase in photosynthetic efficiency. None of the treatments significantly altered community structure following acute exposure, however. The ultraviolet treatments enhanced the toxic effects, which suggests that phototoxicity could have been an important component of the toxicity of Macondo oil (Wade H. Jeffrey, University of West Florida, Pensacola, personal communication, 7 April 2014).

Although bacterial activities are relatively restricted in areas near the site of the Macondo spill because of nutrient limitation (Edwards et al. 2011), biodegradation byproducts (particularly nutrients) may enhance the tolerance of phytoplankton to crude oil. As was evident in a study by Ozhan and Bargu (2014a), the addition of nutrients increased the tolerance of the GOM phytoplankton communities to crude oil. In the same phytoplankton community-based study, Ozhan and Bargu (2014a) examined the potential effects of exposure to LSC oil, Corexit EC9500A, and dispersed oil on enclosed phytoplankton communities under different nutrient regimes. Overall, the addition of LSC oil and Corexit led to a decrease in the number of sensitive species and an increase in more resistant species. The specific responses differed considerably between the two contaminants, however.

Moreover, remarkable differences in phytoplankton succession and community shifts were observed under different nutrient regimes. Phytoplankton communities showed more sensitivity to LSC oil under nutrient-limited conditions. The addition of nutrients to initially nutrient-limited treatments lessened the inhibitory effect of LSC oil in the short term. Centric diatoms benefited most from this enrichment, but pennate diatoms demonstrated considerably greater tolerance to crude oil at low concentrations in nutrient-enriched treatments, whereas dinoflagellates showed relatively higher tolerance in nutrient-limited treatments in uncontaminated waters.

Current limitations and future prospects

The (limited) studies that have been presented or published to date addressing phytoplankton responses to the Macondo blowout indicate that there is evidence of possible stimulation of the phytoplankton, as was demonstrated by the higher chlorophyll concentrations in the northeastern GOM soon after the wellhead was capped. This stimulation could be attributed to intense bacterial activity developed in the photic zone of the GOM during and after the spill (e.g., Hazen et al. 2010, Edwards et al. 2011, Ziervogel et al. 2012). The presence of low-salinity water in the region, however, makes it difficult to discount the importance of riverine inputs (i.e., nutrients) as a factor, although Hu and colleagues (2011) present a strong argument that the FLH anomaly patch observed in the August 2010 MODIS data did not correspond to any river anomaly in 2010 but, rather, coincided with observed and predicted Macondo oil locations. Field-based data suggest that the oil spill could have been toxic to phytoplankton (according to the *P. lunula*-based QwikLite assay; Paul et al. 2013), although laboratory- and microcosm-based studies indicate that the various phytoplankton species have different tolerance levels to the oil and dispersant.

Acknowledging the above conclusions, a dearth of information prevents adequate answers for the following questions regarding the Macondo blowout's impacts on phytoplankton: Which phytoplankton groups or species were stimulated or inhibited by the oil spill (including exposure to Corexit and dispersed oil)? How long did it take for the phytoplankton community to recover? What impacts did alterations to the phytoplankton community have on zooplankton and higher trophic levels? What impacts did alterations to the phytoplankton community have on the microbial community? What impacts did alterations to the phytoplankton community have on the flux of carbon to the benthos, which, in turn, could affect hypoxia?

Undoubtedly, there are many ongoing studies that can help to answer these questions, but there are few remaining options to examine the *in situ* impacts of the oil spill on the phytoplankton community at this late date (one exception being any forthcoming phytoplankton-focused Natural Resource Damage Assessment studies). If one were to attempt to prepare for future oil spills, the following aspects would have to be addressed: baseline data, field samples during and after an oil spill, logistical support for the first two points, mesocosm studies, and enhanced modeling efforts.

Several research groups are collecting phytoplankton data to establish baseline conditions from which future perturbations to pelagic ecosystems can be assessed when such impacts occur. For example, the Coastal Waters Consortium (funded through the Gulf of Mexico Research Initiative) is currently compiling and analyzing phytoplankton and environmental data collected on the Louisiana shelf (west of the Mississippi River) since 1989 to establish baseline conditions and to examine the dynamics of the phytoplankton community over seasonal, annual, and decadal timescales. Samples were collected prior to, during, and following the Macondo spill, but the findings have yet to be published. In addition, long-term monitoring for phytoplankton east of the Mississippi River has also been initiated (James A. Nienow, Valdosta State University, Valdosta, Georgia, personal communication, 7 April 2014). Such efforts as these will be beneficial in assessing both the long-term impacts of the Macondo spill on the pelagic ecosystem and any impacts that may occur in the future.

Measures should be taken to strengthen our capabilities to respond to future, unforeseen oil spills. Part of this effort should include logistical considerations (i.e., short notice ship-time scheduling) and standardized sampling protocols to facilitate a rapid (and maintained) response. As data from the Macondo spill continue to be collected and analyzed, our understanding of and responses to future oil spills will improve as a result.

The study of potential impacts of crude oil on phytoplankton communities is a complicated process. Different crude oils do not affect phytoplankton in identical ways because of the unique compositions of crude oils from different wells or regions. The weathering of the oil can affect its toxicity. The presence of dispersant can make the oil more toxic. Toxicity can vary with temperature and light. Phytoplankton may be more sensitive to oil toxicity under nutrient-limited conditions. Some phytoplankton may be more tolerant of petroleum compounds under low concentrations, whereas different species may be more tolerant under high concentrations. Some phytoplankton species are more sensitive to crude oil exposure than others. Because phytoplankton populations can change quickly on small temporal and spatial scales, it can be difficult to predict how a phytoplankton community as a whole will respond to an oil spill.

Although there have been many laboratory-based studies in which the toxicity of crude oil and its various components (and in the presence of dispersants and under varying environmental conditions) have been examined, there remains much work to be done in terms of field-based (*in situ*) and mesocosm studies to better understand how phytoplankton will respond to an oil spill and how to assess its subsequent impacts on the community (and higher trophic levels). In addition, future model development should incorporate phytoplankton responses to oil spills under various conditions,

thereby providing a tool to help predict and assess crude oil impacts on phytoplankton (and higher trophic levels). Simulations can also be run to test various response options (e.g., the use of Corexit, increased flow of river diversions).

The Macondo blowout demonstrated that there is much that we do not know about how oil spills affect the base of coastal pelagic food webs—the phytoplankton. These gaps in our knowledge can be addressed with proper planning and resources. Then and only then can we adequately gauge what phytoplankton responses to these accidents will be.

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