Impact of Oil Spills on Marine Life in the Gulf of Mexico

EFFECTS ON PLANKTON, NEKTON, AND DEEP-SEA BENTHOS

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ABSTRACT. The Deepwater Horizon (DWH) oil spill was the largest accidental release of crude oil into the sea in history, and represents the most extensive use of chemical dispersants to treat an oil spill. Following the spill, extensive studies were conducted to determine the potential acute and sublethal toxic effects of crude oil and dispersants on a range of planktonic, nektonic, and benthic marine organisms. Organisms such as phytoplankton, zooplankton, and fish were examined via controlled laboratory studies, while others, such as deep-sea benthic invertebrates, which are difficult to sample, maintain, and study in the laboratory, were assessed through field studies. Laboratory studies with marine fishes focused on the sublethal effects of oil and dispersants, and early life history stages were generally found to be more sensitive to these toxins than adults. Field studies in the vicinity of the DWH spill indicate a significant reduction in abundance and diversity of benthic meiofauna and macrofauna as well as visual damage to deep-sea corals. Overall, studies indicate that while the responses of various marine species to oil and dispersants are quite variable, a general picture is emerging that chemical dispersants may be more toxic to some marine organisms than previously thought, and that small oil droplets created by dispersant use and directly consumed by marine organisms are often more toxic than crude oil alone.
INTRODUCTION
The Gulf of Mexico is a semi-enclosed sea that covers more than 1.5 million km², has over 6,000 km of shoreline, receives freshwater from numerous rivers and their watersheds, and has an extensive system of barrier islands. Shallow continental shelf waters make up almost half of the Gulf of Mexico. Its coastal wetlands form essential habitats for migrating birds, and its estuaries serve as nursery areas for estuarine-dependent commercial and recreational fisheries, an important component of the regional economy (Sumaila et al., 2012). The Gulf of Mexico is also a major source of offshore oil and gas in the United States. Nearly half of the total petroleum refining and natural gas processing capacity in the United States is located along the Gulf Coast. Unfortunately, the Gulf of Mexico has also been the location of the two largest marine oil spills in history: the Deepwater Horizon (DWH) spill in 2010 and the Ixtoc I spill in 1979–1980.

The rise of energy demand worldwide has resulted in increasing marine exploration, production, and transportation of crude oil, with resulting increases in the risk of oil spills in the marine environment (NRC, 2003; Dalsoren et al., 2007). Much of the negative impact of oil spills lies in accumulations of the less volatile and less soluble components of crude oil at the sea surface. When these surface oil slicks are carried toward shore, they can cause extensive damage to sensitive intertidal and nearshore environments, such as salt marshes, seagrass beds, mangroves, and coral reefs. Chemical dispersants are often applied to marine oil spills to reduce tension at the oil-water interface and make it easier for physical factors to break up surface oil slicks into small droplets. Smaller droplets allow for more rapid loss of soluble and volatile compounds, and may allow for more rapid consumption of oil by hydrocarbon-degrading bacteria. For surface oil slicks that threaten sensitive coastal habitats, dispersants may be the best option for dealing with oil that cannot be skimmed or burned at the surface. During the DWH spill, dispersants were applied both on surface accumulations of oil and in the deep sea at the wellhead to help break up oil before it reached the surface and lessen the impact to sensitive nearshore environments. By creating small, less buoyant oil droplets at depth, the amount of time needed for oil droplets to reach the surface increased, and some oil remained dispersed at depth (e.g., Camilli et al., 2010).

The DWH spill is a useful case study for assessing the relative environmental costs of treating oil with dispersants compared to using other means to recover it or allowing it to degrade naturally without dispersant application. Laboratory toxicity studies of oil and dispersants on marine organisms are conducted on the water accommodated fraction (WAF) of crude oil and/or on the chemically enhanced water accommodated fraction (CEWAF) that has been enhanced by the addition of dispersants (Jiang et al., 2010). To assess the risks to the marine food web of applying large quantities of dispersant, it is essential to know the lethal toxicity levels of dispersed crude oils to various groups of marine organisms, how they accumulate or depurate the constituents of these complex mixtures, if and how they are passed through the food web to higher trophic levels, and what type of sublethal effects dispersed crude oil have on organisms throughout the marine food web. It is known that oil entered the food web as a result of the DWH spill (Graham et al., 2010), but the processes that control the amount and extent of oil-derived carbon entering marine food webs are largely unknown. With more complete information on the effects of dispersed crude oil on marine life, and the possible transfer of toxic compounds in food webs, it will be possible to better judge the risks and trade-offs involved with extensive use of dispersants during a spill.

TOXIC COMPONENTS OF OIL, DISPERGANTS, AND MIXTURES OF THE TWO
Oil can be toxic to organisms, causing either physical or biochemical injury. Physical injury arises from oil being absorbed, inhaled, or ingested, impairing the ability of a marine organism to perform daily functions. Biochemical injury arises when specific chemical compounds present in oil interact with and cause damage to an organism’s cellular metabolism. The components of oil known to be toxic to marine organisms include volatile organic compounds (VOCs) such as benzene, toluene, ethylbenzene, and xylene, collectively known as BTEX, as well as polycyclic aromatic hydrocarbons (PAHs), which are known for their persistence in the environment. The polar components of oil, which are defined as the nitrogen-sulfur-oxygen (NSO)-containing compounds, have a less established toxicity. However, they can account for ~70% of all oil compounds dissolved in water and are thought to be more toxic to marine organisms and more persistent in the environment than other crude oil components (Y. Liu and Kujawinski, 2015, and references therein). When considering the impact of oil on marine organisms, it is imperative to consider the amount and duration of the oil exposure, as well as the composition and comparative toxicity of the specific oil compounds that are present.

The dispersants used as part of the response to the DWH spill (Corexit 9527 and Corexit 9500A) were tested by the US Environmental Protection Agency (EPA) and found to be no more or less toxic than alternative dispersants studied. The EPA also states that the dispersants alone are less toxic than oil, whereas dispersant-oil mixtures exhibit toxicity similar to oil (USEPA, 2010). Studies examining the toxicity of oil compared to oil and dispersant mixtures are limited, and there
is disagreement as to which is more toxic (e.g., Albers and Gay, 1982, versus Major et al., 2012). The persistence of these dispersant and oil mixtures in the environment (White et al., 2014) highlights the importance of further analysis to establish their toxicity and potential impacts on marine organisms.

**LETHAL AND SUBLETHAL EFFECTS ON PLANKTONIC ORGANISMS**

Understanding the effects of oil and dispersant on planktonic organisms is important due to their central role in primary production in coastal and open ocean environments. Microscopic, rapidly reproducing, single-celled phytoplankton that are the main source of primary production in the ocean are rapidly consumed by small protozoans and metazoans collectively known as zooplankton. These grazers are typically short lived, have high reproductive rates, and are in turn rapidly consumed by higher trophic levels within marine food webs, providing the potential for rapid transfer of bioaccumulated toxic compounds to higher trophic levels. Recent studies demonstrate that crude oil, chemical dispersants, and dispersed oil can be toxic to a wide range of marine organisms, and that dispersed oil can be directly ingested by many zooplankton species (Lee et al., 2012).

Phytoplankton assemblages in the Gulf of Mexico are composed of numerous taxa that vary both spatially and temporally, making generalizations on the impacts of oil on phytoplankton communities particularly challenging. Numerous studies have been performed to determine the toxic effects of crude oil on phytoplankton (e.g., N. Liu et al., 2006), and estimates of toxicity to phytoplankton vary widely with the taxa studied. Exposure to a mix of both crude oil and dispersants, compared to each alone, can lead to increased toxicity in some phytoplankton species (Ozhan and Bargu, 2014). Diatoms have generally been found to be more sensitive than other phytoplankton groups to crude oil and/or oil-dispersant mixtures (Hook and Osborn, 2012), suggesting that oil toxicity may impact both phytoplankton community composition and abundance (Hallare et al., 2011). Although exposure to crude oil often reduces phytoplankton productivity and growth, some species are reported to be highly tolerant of oil exposure, and in some cases it may even stimulate their growth (Jiang et al., 2010; Hallare et al., 2011). Phytoplankton may also be important contributors to marine oil snow (Passow et al., 2012). These slowly sinking aggregates may provide a mechanism for toxic oil chemicals to be incorporated into higher trophic levels, in both the water column and the benthos.

Marine protozoa are often the major grazers on phytoplankton in the sea and are important components of marine food webs (Calbet, 2008). However, there have been relatively few studies of the effects of oil and dispersants on marine protozoa; many species are challenging to culture in the laboratory, and characterization of diverse protozoan communities in field samples can be tedious and time consuming. Though field studies of the impacts of oil spills on protozoan communities are limited, it has been shown that crude oil can reduce the abundance of planktonic ciliates (Koshikawa et al., 2007), and marine ciliates have been observed directly taking up crude oil droplets in the laboratory and the field (Andrews and Floodgate, 1974). Additionally, correlations between increased abundance of heterotrophic dinoflagellate blooms (Noctiluca sp.) and oil spills have been reported (Févre, 1979).

Planktonic copepods are key links in marine food webs. They consume both phytoplankton and protozoan grazers (Banse, 1995), and copepods are in turn fed upon by many different species, ranging in size from other zooplankton to baleen whales. Many fish species consume them (Castonguay et al., 2008), which places copepods only one or two trophic levels away from species consumed by humans. This has resulted in many studies investigating the toxicological effects of crude oil and/or dispersants on various zooplankton groups. Decreases in zooplankton populations after oil spills have been reported (Guzman del Proo et al., 1986). Studies demonstrate that copepods will ingest emulsified oil droplets in the laboratory, that signatures of hydrocarbons can remain in their bodies for extended periods (Gyllenburg, 1981), and that exposure to crude oil and chemical dispersants can lead to acute toxicity in copepods. The life cycles of a majority of marine invertebrate species include planktonic larvae (Thorson, 1950). Larval stages of marine invertebrates are generally found to be very sensitive to oil toxic chemicals (Jiang et al., 2010) and chemical dispersants (Goodbody-Gringley et al., 2013), and larval stages are often more sensitive to these toxins than adult forms (Almeda et al., 2014b).

Sublethal exposure of copepods to crude oil toxins may result in decreases in feeding (Cowles and Remillard, 1983), egestion (Almeda et al., 2014a), and reproduction (Olsen et al., 2013). Oil toxicants have also been reported to alter swimming behavior (Cohen et al., 2014) and decrease mating success in planktonic copepods (Seuront, 2011). Even subtle changes in copepod behavior may make them more vulnerable to predation. Selective bioaccumulation of five PAHs has been measured in zooplankton exposed to sublethal levels of crude oil (Almeda et al., 2013b). Sublethal exposure to crude oil toxicants could cause these organisms to become more susceptible to predation, leading to enhanced trophic transfer of toxic PAHs in marine ecosystems.

Further studies of the effects of crude oil and dispersants on zooplankton have been conducted since the DWH spill. A recent study of several species of cultured marine protozoa indicates that the dispersant Corexit 9500A can be highly toxic, especially to ciliates, and that chemically dispersed crude oil can be more toxic to these protists than crude oil alone (Almeda et al., 2014d). Heterotrophic dinoflagellates are generally less sensitive
to crude oil exposure and have also been shown to ingest and defecate physically or chemically dispersed crude oil droplets (1–86 μm in diameter). At crude oil concentrations of 1 μL L–1, the heterotrophic dinoflagellate species *Noctiluca scintillans* and *Gyrodinium spirale* ingested approximately one-third of their biomass equivalent in oil per day and continued to grow in culture (Almeda et al., 2014c; Figure 1). A study of three species of marine copepods found that both crude oil and chemical dispersant were acutely toxic to copepods at low concentrations. Chemically dispersed oil droplets were ingested by the copepods (Almeda et al., 2014a), and crude oil droplets have been found in the fecal pellets of copepods exposed to physically or chemically dispersed crude oil, which may produce an important flux of crude oil from the water column to the benthos (Almeda et al., 2015: Figure 2). Selective biomagnification of PAHs has been reported in copepods, but adding another link in the food chain (phytoplankton–protozoa–copepod) resulted in lower accumulation of PAHs in copepod tissues (Almeda et al., 2013a), suggesting that biomagnification of PAHs in marine food webs may be limited.

One of the major adaptive advantages of planktonic larvae of benthic invertebrates is the ability of these motile larvae to disperse to new habitats. Some invertebrates produce non-feeding lecithotrophic larvae that depend on internal nutrients provided to the egg (yolk) to keep them alive for short periods until they metamorphose into their adult forms, while planktotrophic larvae can feed on phytoplankton and/or zooplankton during these dispersal stages and therefore survive for longer periods of time without risking starvation. Recent studies show that planktotrophic invertebrate larvae also directly consume tiny dispersed oil droplets. As a result, physically and chemically dispersed crude oil is more acutely toxic to these larvae than to lecithotrophic larvae that do not consume oil droplets but are mainly exposed to dissolved oil toxicants (Almeda et al., 2014b). Both the planktotrophic species and the lecithotrophic species tested exhibited decreased growth rates when exposed to chemically dispersed crude oil toxins (Almeda et al., 2014b).

Many toxicity experiments on planktonic organisms are carried out under laboratory conditions using low intensity artificial lighting. Even when incubations are performed outdoors under natural sunlight, the containers used in experiments are often not transparent to ultraviolet light. The use of quartz glass bottles can significantly increase the exposure to ultraviolet light and therefore affect the toxicity of crude oil to zooplankton (Almeda et al., 2013b, 2016). For planktonic organisms that live in shallow waters, or spend much of their time in surface waters during daytime, it is important to consider the effects of ultraviolet exposure to accurately predict the impacts of crude oil toxons on these organisms.

**LAB STUDIES: LETHAL AND SUBLETHAL EFFECTS ON FISH, REPRODUCTION, BEHAVIOR, PHYSIOLOGY, AND LARVAE**

The most direct method for assessing the relative sensitivity of fish species is standardized dose response survival (or lethality) toxicity tests. Unfortunately, the difficulty of obtaining relevant life stages of fish native to the Gulf of Mexico makes such experimentation and data limited. This is further complicated by the variable chemical composition of different crude oils and the inconsistent quantification and reporting methods employed across studies. For example, oil toxicity has been reported in terms of nominal percent WAF, total petroleum hydrocarbons (TPH), and the sum of polycyclic aromatic hydrocarbons (ΣPAH). Nonetheless, several trends can be observed. The most apparent is that embryonic and larval life stages are the most sensitive. These fish exhibit toxicity in low µg L–1 ΣPAH concentrations, but this may vary by up to an order of magnitude. In particular, recent work on the embryonic stage of a fast-developing pelagic species,

![FIGURE 1. Ingestion of crude oil droplets by marine protozoa. Microscope images of the heterotrophic dinoflagellate *Noctiluca scintillans* with food vacuoles containing crude oil droplets (left) and the same cell under ultraviolet illumination, showing oil droplets fluorescing brightly (right). Photo credit: Rodrigo Almeda](image)
mahi-mahi (*C. hippurus*), demonstrates acute toxicity at concentrations as low as 8.7 µg L⁻¹ ΣPAH₅₀ (Esbaugh et al., 2016), and this extends to several other pelagic species based on similar sublethal sensitivities (Incardona et al., 2014).

The majority of studies examining the effects of oil exposure on fish following the DWH spill focused on sublethal endpoints. The most well characterized effect of oil on fish involves changes in heart structure and function in the embryonic stage (see review by Collier et al., 2013). The effects can vary depending on the species and exposure concentration; however, they are generally defined by the occurrence of pericardial edema, and this morphological deformity is often accompanied by changes in embryonic cardiac function. Recent work shows dose-dependent occurrences of edema in yellowfin tuna, bluefin tuna, and mahi-mahi embryos (Figure 3), accompanied by reduced heart rate and atrial contractility (Incardona et al., 2014; Esbaugh et al., 2016). In addition to these hallmark symptoms, the cardiotoxic effect may be accompanied by spinal curvature, fin-fold damage, and craniofacial malformations (Incardona et al., 2014).

Impaired cardiovascular development in fish embryos is also hypothesized to reduce individual cardiovascular performance in later life. Studies on several species demonstrate that transient 48 h embryonic exposure leads to reduced swimming performance in later life (Hicken et al., 2011). Acute WAF exposure in post-larval stages has also been shown to disrupt swim performance (Mager et al., 2014), but these effects do not manifest until 30 µg L⁻¹ ΣPAH₅₀ compared to the observed effects at 1.2 µg L⁻¹ ΣPAH₅₀ for embryonic exposure.

The effect of weathering on oil toxicity in fish has been a controversial subject. It was expected that weathered oil should exhibit reduced toxicity, owing to the progressive loss of the highly soluble low molecular weight PAHs and volatiles that purportedly drive toxicity (Di Toro et al., 2007). Nonetheless, experiments investigating toxicity in several species of larval fish consistently demonstrate that weathered WAFs result in increased toxicity (e.g., Esbaugh et al., 2016). It is now clear that the most sensitive endpoints for toxicity in fish, larval cardiotoxicity and survival, are not driven by a narcosis mode but rather by higher molecular

**FIGURE 2.** Small, dispersed oil droplets can be directly consumed by copepods. Some of this oil remains in their fecal pellets, and these sinking pellets may provide an important pathway for dispersed oil in the water column to sink to the bottom. *Almeda et al. (2015)*
weight three-ring PAHs. While it is difficult to fully attribute toxicity to three-ring PAHs in all species, it seems that uncertainty about the toxic mode of action likely explains the discrepancies between observed and expected sensitivity to weathered oils.

A number of additional sublethal endpoints have also been described, such as growth and reproduction. Southern flounder (*P. lethostigma*) exhibited dose-dependent growth inhibition when exposed to oiled sediments (Brown-Peterson et al., 2015), and both larval and juvenile seatrout (*C. nebulosus*) exhibited growth inhibition during acute single dose CEWAF and HEWAF (high energy water accommodated fraction) exposures (Brewton et al., 2013). Tissue histopathology is also a common consequence of oil exposure (see review in Collier et al., 2013). In relation to the DWH spill, studies on southern flounder and alligator gar, *A. spatula*, demonstrate histopathology in the liver and gill, as well as reduced lymphocyte and granulocyte density (Brown-Peterson et al., 2015; Omar-Ali et al., 2015). Field studies show similar histopathology in menhaden species (*genus Brevoortia*) collected following the spill (Bentivegna et al., 2016).

Dispersant is a known fish toxicant, including for species native to the Gulf of Mexico, but there is little evidence of additive or synergistic toxicity when combined with oil. Direct comparisons of HEWAF and CEWAF preparations demonstrate similar or reduced levels of toxicity in terms of survival (Hemmer et al., 2011) and cardiotoxicity (Esbaugh et al., 2016). However, dispersant may impact the chemical profile of a WAF, though this is not often considered when assessing toxicity. Recent work highlights this difficulty whereby embryonic survival is affected by dispersant in mahi-mahi when expressed as ΣPAH but no difference is observed when expressed as dissolved ΣPAH (Esbaugh et al., 2016). Nonetheless, the available evidence strongly suggests that oil toxicity alone far exceeds any additive or synergistic impacts of oil with dispersant for larval fish.

Photo-enhanced toxicity occurs when certain wavelengths of light enhance the observed toxicity of a compound. It is now well documented that larval fish exhibit photo-enhanced PAH toxicity, with survival influenced by the amount and type of ultraviolet light exposure (e.g., Barron et al., 2003). Photo-enhanced toxicity can reduce embryonic survival by orders of magnitude. Importantly, only certain PAHs are classified as phototoxic, which raises an additional level of complexity regarding the exact chemical composition of different oils. The importance of considering photo-enhanced toxicity during environmental assessments has also been highlighted owing to the location of many fish spawning habitats. Specifically, the buoyant eggs of pelagic fish and the shallow spawning habitat of many nearshore species are of particular concern, as these areas are likely to receive higher intensities of ultraviolet light; however, water turbidity may mitigate some of this concern in nearshore habitats.

**IMPACTS OF OIL AND DISPERSANT ON DEEP-SEA BENTHOS**

Lab and field-based studies are necessary to assess the impact of oil on deep-sea benthos (DeLeo et al., 2016; Fisher et al., 2014a), with the latter providing unique insight into the potential effects of oil on the larger deep-sea ecosystem. In addition to visible signs of damage, biological indicators, such as changes in species abundance and diversity of organisms, are primarily used to assess impact. Correlation to chemical indicators provides important environmental context and may include analysis of the quantity and composition of oil as well as changes in the concentrations of relevant metals.

Visible damage to organisms in the deep sea was most evident in coral communities that were first observed in November 2010, 11 km from the wellhead. Corals imaged by the remotely operated vehicle (ROV) *Jason II* or the Deep Submergence Vehicle *Alvin* exhibited signs of stress, including tissue loss, excess mucous production, enlarged sclerites, and bleached commensal ophiuroids (White et al., 2012). A brown flocculent material covering the corals was later found to contain oil from the DWH spill (White et al., 2012) and microbes affiliated with oil-degrading bacteria (Simister et al., 2016). Changes in the species diversity and abundance of macrofaunal and meiofaunal communities associated with sediments adjacent to the corals also indicate oil spill impacts (Fisher et al., 2014a). Observations via high-resolution imaging of individual corals made over the next 16 months revealed that while recovery of

*FIGURE 3. Representative image of a 48-hour post fertilization mahi-mahi larva exhibiting pericardial edema (red tracing) following exposure to high-energy water-accommodated fractions of oil. Photograph courtesy of Ed Mager and Martin Grosell*
individual corals was possible, the extent of the initial visible impact of oil correlated to lasting damage and secondary colonization of hydrozoans on the dead parts of the corals (Hsing et al., 2013; Fisher et al., 2014b).

Montagna et al., (2013) determined the impact of oil on soft-bottom benthic invertebrates by analyzing the abundance and diversity of macrofauna and meiofauna in deep-sea sediments from 68 locations. This analysis indicates that severe reduction of faunal abundance and diversity extended 3 km from the wellhead in all directions, and moderate impacts extended 17 km toward the southwest and 8.5 km toward the northeast. In the northeastern Gulf of Mexico, a decrease in the density of benthic foraminifera in sediments correlated to changes in the concentration of the redox-sensitive metals Mn, Re, and Cd, indicating that sediments had become more reducing in response to increased sedimentation following the DWH spill (Hastings et al., 2016). Lower species diversity and abundance following the DWH spill was also observed for other communities, including epibenthic and demersal megafauna (obtained from seafloor surveys by ROVs; Valentine and Benfield, 2013), and for seaweeds and decapod crustaceans associated with crustose benthic marine algae (Felder et al., 2014).

CONCLUSIONS, CHALLENGES, AND FUTURE WORK

The research funding that began after the DWH spill in the Gulf of Mexico led to a substantial increase in knowledge regarding the toxic effects of crude oil, chemical dispersant, and dispersed oil on marine life of subtropical waters. Extensive field studies assessed the damage to the fauna and flora of the Gulf of Mexico, and numerous controlled laboratory experiments improved basic understanding of the toxicity of oil and dispersants to a wide range of marine organisms. In addition, extensive studies were carried out to improve understanding of how crude oil and dispersant-treated oil behave in the marine environment, and how physical processes affect the transport of these substances. A remaining challenge is to incorporate this new knowledge into predictive models that will assist managers and policymakers in determining how best to respond to future oil spills in order to minimize their impacts on the environment.