Oil Impacts on Coastal Wetlands: Implications for the Mississippi River Delta Ecosystem after the *Deepwater Horizon* Oil Spill

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On 20 April 2010, the Deepwater Horizon *explosion, which released a* US government–estimated *4.9 million barrels of crude oil into the Gulf of Mexico, was responsible for the death of 11 oil workers and, possibly, for an environmental disaster unparalleled in US history. For 87 consecutive days, the Macondo well continuously released crude oil into the Gulf of Mexico. Many kilometers of shoreline in the northern Gulf of Mexico were affected, including the fragile and ecologically important wetlands of Louisiana's Mississippi River Delta ecosystem. These wetlands are responsible for a third of the nation's fish production and, ironically, help to protect an energy infrastructure that provides a third of the nation's oil and gas supply. Here, we provide a basic overview of the chemistry and biology of oil spills in coastal wetlands and an assessment of the potential and realized effects on the ecological condition of the Mississippi River Delta and its associated flora and fauna.*

Keywords: wetlands, environmental science, ecology, coastal ecosystems, microbiology

The uncontrolled blowout of the Macondo wellhead, located at Mississippi Canyon Block 252, which occurred on 20 April 2010 during the completion of drilling by the *Deepwater Horizon* (DWH) drilling platform, is potentially one of the largest environmental disasters ever experienced in the United States, and, without question, the largest marine oil discharge. The release of a US government-estimated 4.9 million barrels of oil exposed the nation's largest and most productive wetland–estuarine environment to an unprecedented level of environmental impact (National Commission on the BP *Deepwater Horizon* Oil Spill and Offshore Drilling 2011). The coastal wetlands of the Mississippi River Delta ecosystem, which constitute almost 40% of the coastal wetlands of the 48 conterminous United States, is of special concern because of the multitude of environmentally and economically important services that they supply to the northern Gulf of Mexico (GOM) and to the entire United States. These wetlands provide the base for such ecosystem services as storm protection, water quality enhancement, faunal support, and carbon sequestration. Approximately 30% of the United States' commercial fishery production is dependent on these wetlands, and ironically, they protect an oil and gas infrastructure that provides one-third of the nation's oil and gas supply and 50% of the nation's refining capacity.

Of course, the DWH spill is not the first to affect coastal wetlands. In the United States alone, multiple smaller spills occur each year. However, large spills that result in significant coastal wetland impacts do occur periodically (table 1). Two of the earliest global spills of note are the West Falmouth release of approximately 4400 barrels of fuel oil from the barge *Florida* into Buzzards Bay, Massachusetts, and the spill from the tanker *Amoco Cadiz*, which discharged 1.6 million barrels of crude along the shoreline of Brittany, France. Both spills affected coastal marshes. In the case of the *Amoco Cadiz* event, animal and plant recovery occurred within 8 years where the soil had not been removed during oil cleanup (Baca et al. 1987). In contrast, 40 years after the West Falmouth spill, impacts were still evident (Culbertson et al. 2008). Marsh recovery after an oil spill can vary greatly (table 1), depending on a variety of factors, which are described further below. The aim of this overview is to

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Table 1. Comparison of some scientifically documented oil spills that have affected coastal wetlands.

Spill	Date	Volume (gallons[a])	Oil type	Dominant vegetation	Impacts	Recovery	Reference
Super-tanker, *Amaco Cadiz* spill, Brittany, France	March 1978	67,200,000	Crude	*Juncus maritimus*, *Halimione portulacoides*, *Triglochin maritima*, *Salicornia* spp.	Rapid erosion after surface oiled sediment removal up to 50 cm; 12 years later, vegetation area was reduced by 22%–38%	Plant recovery by invasion from annuals and rhizome spreading of perennials in 8 years	Baca et al. 1987, Gilfillan et al. 1995
Pipeline rupture, Nairn, Louisiana	April 1985	12,600	Crude	*Spartina alterniflora*, *Spartina patens*, *Distichlis spicata*	64% reduction in live vegetation cover three months after spill	Near total vegetative recovery 4 years after the spill	Mendelssohn et al. 1990, Hester and Mendelssohn 2000
Barge *Florida*, West Falmouth, Massachusetts	September 1969	184,900	No. 2 fuel	*S. alterniflora*, *S. patens*	Four decades after the spill, stem density and biomass of *S. alterniflora* still reduced in oiled areas; unconsolidated sediments, increased topographical variation, and, ultimately, loss of salt marsh habitat	Only 100 of the original 595,000 kg of spilled oil still in salt marsh sediment 40 years later; effects on large-scale ecosystem functions were still evident	Culbertson et al. 2008
Pipeline rupture, Arthur Kill, New York	January 1990	660,450	No. 2 fuel	*S. alterniflora*	95% of the surface area denuded of vegetation by oil at unplanted reference sites remained unvegetated 7 years after the spill	3 years after planting, the aboveground biomass at two of the three restoration sites was comparable to the biomass at existing and restored eastern North American salt marshes	Bergen et al. 2000
Pipeline rupture, Swanson Creek, Maryland	April 2000	140,000	Mixture of No. 6 and No. 2 fuel	*S. alterniflora*, *Spartina cynosuroides*	7 years later, stem density and stem height significantly lower in oiled sites for *S. alterniflora*; belowground biomass significantly lower in *S. cynosuroides* oiled sites	The oil had lost 22%–76% of its initial PAH content after 7 years; 25% of the soils in the marsh are expected to be toxic	Michel et al. 2009
Storage tank rupture, Bahía Las Minas, Panama	April 1986	2,100,000	Crude	*Rhizophora mangle*	Mature trees died over large areas in a few months; over 4 years, dead trees decayed, erosion of the associated oiled sediments	Over 3 years after the spill, dense growths of young seedlings occur in much of the deforested areas	Duke et al. 1997
Three-vessel collision, Tampa Bay, Florida	August 1993	300,000	Mixture of No. 6 fuel, gasoline, Jet-A fuel, and No. 2 fuel	*Avicennia germinans*, *R. mangle*, *Laguncularia racemosa*	9 months after the spill, significantly more juvenile red and black mangroves dead by leaf and shoot oil coating; adult red mangroves defoliated and died in areas of greatest stranded oil	2 years later, standing crop and production dropped strongly with greater oiling, indicating substantial sublethal injury	Levings and Garrity 1995, Levings and Garrity 1997
Oil well blowout, *Deepwater Horizon* event, northern Gulf of Mexico	April 2010	205,800,000	Macondo sweet crude	*S. alterniflora*, *Juncus roemerianus*, *A. germinans*, *Phragmites australis*	Shoreline vegetation from the Chandeleur Islands to Point Au Fer variably impacted by the oil	Not yet quantified	National Commission on the BP *Deepwater Horizon* Oil Spill and Offshore Drilling 2011; IAM and QL, personal observations

[a]There are 42 gallons of oil in 1 barrel.
cm, centimeters; kg, kilograms; PAH, polycyclic aromatic hydrocarbons.

provide a context from which the public and the scientific communities can better understand the realized and potential impacts and prospects for future recovery related to the DWH spill on coastal wetlands and their associated natural resources. Below, we summarize the general knowledge of oil spill impacts on coastal marshes—and, when possible, the impacts specific to the DWH spill—relative to the chemistry of oil and its related toxicity; the capacity of microbial processes to degrade oil and reduce toxicity; the responses of wetland vegetation, benthic biota, and marsh-dependent fishery resources to oil; and impacts on ecosystem services on which humans rely (figure 1).

Why oil is toxic: Its chemical composition and how it changes over time

The toxicity of oil and its impact on biota are primarily determined by its chemical composition. Oil and natural gas are derived from biological materials whose composition has been modified by diagenesis over millions of years to produce the complex mixture of hydrocarbon and nonhydrocarbon compounds that constitute these fossil fuels. Typically, crude oils are all made up of the same types of molecular hydrocarbons. However, the proportion of specific molecules in crude oil from a given reservoir depends on the reservoir's location, depth, and age.

The four classes of hydrocarbons in crude oil are saturates, aromatics, asphaltenes, and resins (Leahy and Colwell 1990); saturates and aromatics generally dominate. Saturate hydrocarbons, which contain straight-chain, branched, and cyclic structures, constitute the greatest percentage of crude oil. The majority of crude oils encountered in oil spills contain straight-chain hydrocarbon molecules, ranging from single-carbon methane to molecules that contain in excess of 35 carbons, with associated branched and cyclic hydrocarbon structures. Some of the saturate C19–C30 cyclic hydrocarbons are particularly resistant to biodegradation and serve as crude-oil biomarkers. Asphaltenes—large-molecular-weight hydrocarbons containing trace amounts of nickel and vanadium—are even more resistant to microbial degradation and are commonly used as roofing tar and road asphalt.

In contrast to saturates, the aromatic hydrocarbons of crude oils consist of relatively simple single-ring structures, such as benzene, and more-complex cyclic aromatic structures with multiple condensed rings, called *polycyclic aromatic hydrocarbons* (PAHs). The unique structure and bonding of PAHs increase their solubility and, therefore, their ability to influence various enzyme-mediated reactions in biota. Because of their toxic and mutagenic effects, aromatic compounds are the most environmentally significant of all compounds in crude oils.

When oil enters the environment from spills, ruptures, or blowouts, it undergoes continuous compositional changes associated with weathering (figure 2). Weathering processes include evaporation, dissolution, emulsification, sedimentation, microbial oxidation, and photooxidation. Weathering changes the oil's physical and toxic properties. Fresh oil is more volatile, contains more water-soluble components, floats, is not very viscous, and easily disperses from the source. Therefore, freshly spilled oil is the most environmentally significant type of oil. Weathered oil initially loses volatile components, which are also the most water-soluble components, and the oil becomes more viscous and more likely to coagulate as opposed to spreading out in a thin film. Over time, weathering continues to change the composition of oil until it degrades in the environment, leaving behind only small quantities of residue (e.g., tar balls; figure 2). Typically, during weathering, much of the oil (especially heavier oil) will mix with water and emulsify, forming a viscous mixture that is resistant to rapid weathering and more difficult to remediate.

Oil can cause environmental damage through several mechanisms, including the toxicity associated with ingestion or absorption through the biota's respiratory structures or skin; coating or smothering, which affects gas exchange, temperature regulation, or other life-supporting processes; and oxygen depletion by microbial processes associated with oil degradation. Weathering changes the effectiveness of these mechanisms (toxicity, routes of exposure, bioavailability) for causing environmental impacts and, in general, lessens the opportunity for damage.

Most of the oil from the DWH event that reached coastal marshes had been extensively weathered (Reddy et al. 2011). As such, the initial considerations of the oil impact were focused on injury from coating of the biota and, to a lesser extent, oil-induced oxygen-deficiency stress in already hypoxic areas. Because weathered oil does not have a significant route of exposure from dissolution, its potential for toxic impacts is generally lessened compared with the impacts of fresh oil. Nonetheless, the toxic effects of the DWH oil on one fish species have been documented (Whitehead et al. 2011). Benthic animals that are bulk-deposit feeders could also consume oil in this weathered state from the sediment and be exposed via ingestion (Muijs and Jonker 2010). Regardless, direct oil toxicity to flora and fauna cannot be ruled out, given the variable extent of oil weathering.

Microbial processes: Key to oil degradation and reduced toxicity

The chemical composition of oil and its toxicity are not stable over time but change, in part, because of microbial processes, the primary biological means by which oil is degraded in wetlands. Microbial degradation activity in wetlands depends primarily on the type and concentration of petroleum hydrocarbons and environmental factors such as oxygen, nutrients such as nitrogen and phosphorus, salinity, and pH. Surface waters and marsh sediments contain a high diversity of microorganisms. This rich diversity allows for maximum efficiency in resource (especially carbon) utilization and degradation—whether it is petrogenic or not—under changing environmental and nutrient-input conditions.

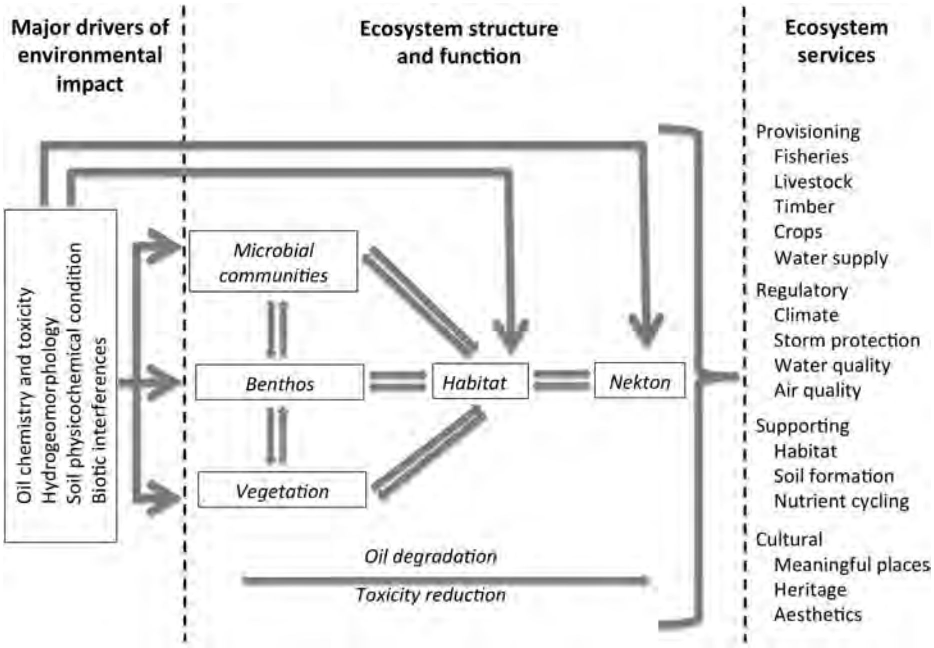

Figure 1. The drivers of environmental impacts during an oil spill include the oil, which changes in composition and toxicity over time, and other stressors and disturbances acting on the ecosystem. The environmental drivers may influence coastal wetlands directly by affecting the habitat or indirectly by way of various interacting ecosystem components. The final outcome may be expressed at higher trophic levels, such as fisheries, and in the numerous wetland-derived ecosystem services on which society relies. We provide an overview of the impacts of the Deepwater Horizon *oil spill from this theoretical context.*

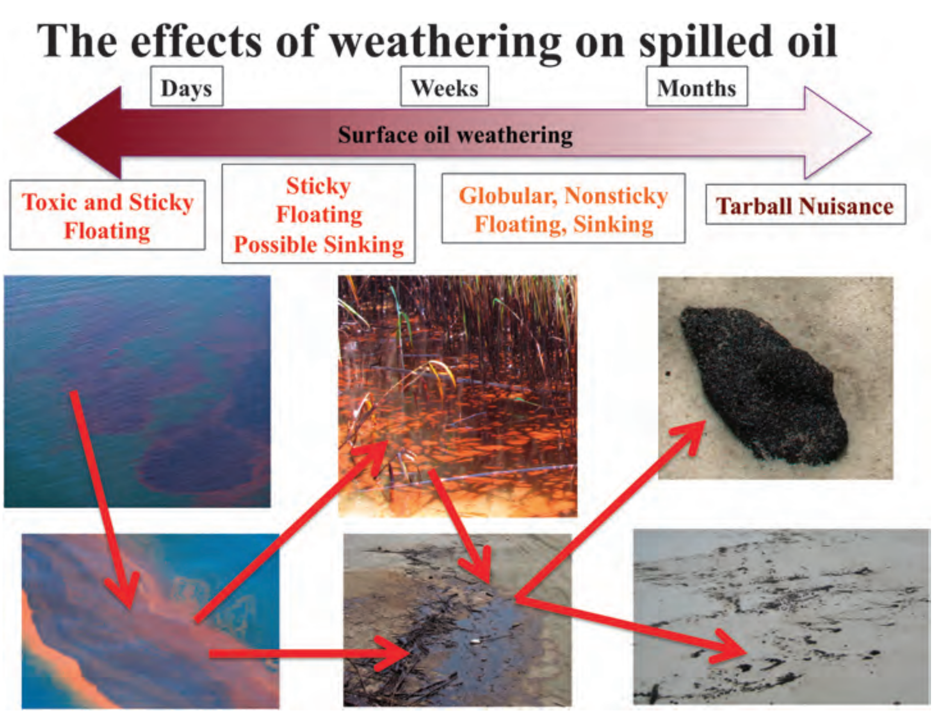

Figure 2. Stages in the weathering of spilled oil from the Macondo well. Photographs: National Oceanic and Atmospheric Administration.

Microbes generally degrade the complex mixture constituting crude oil by first metabolizing the linear alkanes, followed by the branched alkanes, small aromatics, and cyclic alkanes and, finally, by performing a limited degradation of the high-molecular-weight PAHs. The relative abundance of various components in complex petroleum hydrocarbon mixtures shapes the microbial community structure after contamination. Changes in the types of organisms present in sediments or surface waters occur as a result of the sequential degradation of petroleum constituents and the abundance of compounds that are toxic to microbial populations (e.g., heterocyclics, naphthenic acids).

PAHs are the most toxic contaminants and are quite persistent in marshes. The highest levels generally occur below the sediment surface, where there is limited oxygen and a concomitant shift from aerobic to anaerobic bacterial taxa. In a heavily contaminated mangrove swamp, PAH concentrations increased with increasing substrate depth and decreasing oxygen content (Li et al. 2009). PAH-degrading anaerobic bacteria have been identified in contaminated wetland sediments, but given their low oil-degradation capability, it is unlikely that anaerobic bacteria could greatly reduce PAH contamination, except at low concentrations of PAH.

Alternatively, fungi and yeasts play a lesser but still potentially significant role in the biodegradation of hydrocarbons. The advantages of fungal degradation in salt marshes include the ability of hyphae to penetrate through anoxic sediment aggregates or hydrophobic environments. Many fungi can transform hydrocarbons into oxidized derivatives, and a few strains are able to cleave aromatic rings. Several fungal genera are able to remediate soil contaminated with oil. Yeast can also degrade mixtures of both short- and long-chained alkanes found in crude oil (Ijah 1998).

Of the extrinsic environmental factors regulating crude-oil degradation in coastal wetlands, nutrient availability (particularly of nitrogen; Jackson WA and Pardue 1999) and flooding regimes (Shin et al. 2000) are critical controls. For example, the flooding regime of an area exerts a major influence on the biodegradation of crude oil in salt marsh sediments: significant degradation of crude oil through both sulfate reduction and aerobic respiration, the latter of which occurs when the surface of the salt marsh is exposed to the atmosphere (Shin et al. 2000). Flooding, which promotes anaerobic conditions in sediments, hinders hydrocarbon breakdown. However, other studies have demonstrated the breakdown (though often slower) of crude-oil components under anaerobic conditions (Widdel and Rabus 2001). Hydrologic regimes could therefore be expected to influence the rates of crude-oil degradation, and one might anticipate the degradation of aromatic components, which break down faster under aerobic conditions, to be more affected by flooding regimes than are the saturate components.

Nutrients are known to strongly regulate crude-oil or hydrocarbon degradation because petroleum hydrocarbons provide little regenerated nitrogen or phosphorus when they mineralize. Therefore, their mineralization increases carbon:nitrogen and carbon:phosphorus ratios, which hinders further microbial production (Leahy and Colwell 1990). The addition of crude oil to salt marshes can stimulate nitrogen fixation and can drive the system to phosphorus limitation (Griffiths et al. 1982, Gaur and Singh 1990). Although nutrient addition could accelerate microbially mediated hydrocarbon breakdown, the resulting long-term effects on the marsh could be negative (altering nutrient cycling and plant species composition and potentially resulting in eutrophication and oxygen depletion).

Crude-oil deposition can be expected to alter wetland microbial processes and, hence, marsh biogeochemistry (Leahy and Colwell 1990, Shin et al. 2000). A complex suite of microorganisms can use a range of electron acceptors (e.g., oxygen, nitrate, sulfate, iron oxyhydroxides) to degrade saturated and aromatic hydrocarbons (Widdel and Rabus 2001). Typically, crude-oil exposure reduces microbial diversity and increases the abundance of taxa that are able to utilize these unique carbon sources. As such, greater availability of crude-oil-derived carbon and its subsequent oxidation will increase microbial production (So and Young 2001) and the flux of carbon dioxide from marshes. Increased production rates of methane, a potent greenhouse gas, are also possible, because some linear alkanes (e.g., hexadecane) can be converted to methane under anaerobic conditions (Widdel and Rabus 2001). The effects of spilled oil on important microbial processes such as nitrogen fixation, coupled nitrification–denitrification, and sulfate reduction could modify nutrient cycling in oil-affected marshes. Although the experimental addition of crude oil has a negative impact on the overall microbial community composition, it stimulates sulfate-reduction rates (Suárez-Suárez et al. 2011) and enhances the diversity of microorganisms that degrade linear and aromatic oil components (Abed et al. 2011). Nitrogen fixation and denitrification rates, however, can be strongly inhibited by long-term exposure to crude oil (Griffiths et al. 1982), even though some denitrifiers are known to metabolize oil-derived substrates like toluene or ethylbenzene (Champion et al. 1999). By affecting microbial processes, petroleum hydrocarbons can modify nutrient cycling and oil detoxification and can thereby influence vegetation responses.

Wetland vegetation: The responses of foundation species to oil

Wetland vegetation is the ecosystem component providing the foundation for wetland structure and function on which many important ecosystem services rely. Therefore, an understanding of the impact of oil on wetland vegetation is particularly important. Vegetation responses to petroleum hydrocarbons and the vegetation's capacity to recover are dependent on a variety of factors both intrinsic to the plant species and specific to the spill event. Because spills occur under different chemical, environmental, and biotic conditions, impacts and recovery trajectories can vary greatly and can be difficult to predict. The primary determinants of vegetation responses to petroleum hydrocarbons are (a) the toxicity of the oil, which is itself dependent on the type of oil, the amount of weathering, and the extent of plant coverage; (b) the oil's amount of contact with and penetration of the soil; (c) plant species composition; (d) oiling frequency; (e) the season of the spill; and (f) cleanup activities (Lin and Mendelssohn 1996, Hester and Mendelssohn 2000, Pezeshki et al. 2000).

The type of oil is a primary determinant of toxicity. Heavy crude oils, such as San Joaquin or Venezuela crude, which are composed of small concentrations of low-molecular-weight alkanes and aromatics, have a small amount of direct toxicity to plants (figure 3a), whereas light crudes, such as South Louisiana crude, which has relatively high concentrations of lighter-weight hydrocarbons, can cause necrosis and plant mortality on contact (figure 3b). Of course, even highly toxic refined products such as diesel, if they are weathered enough, will eventually lose toxicity, but the less-toxic residuals can still coat vegetation (figure 3c). This condition prevents photosynthesis, thereby impairing the assimilation of carbon used for growth and transpiration, which promotes evaporative cooling. The frequency of repetitive oiling of vegetation is also an important determinant of the ultimate injury; repetitive oiling depletes the underground nutrient reserves used to generate new shoots after successive reoilings. The time of the year in which an oil spill occurs also influences the spill's impacts on plants. Spills during colder periods, when the plants have a lower metabolism or are dormant, have a reduced impact relative to oil exposure during warmer seasons (Alexander and Webb 1985). However,

Figure 3. (a) **Distichlis spicata** *growing in low-toxicity, heavy San Joaquin crude oil in Suisun Bay, California. (b) South Louisiana crude oil causes direct toxicity to* **Salicornia bigelovii** *along a barrier shoreline. (c) San Joaquin crude smothers the stems of* **Schoenoplectus californicus** *along Suisun Bay, causing plant mortality. (d) When oil penetrates marsh soil, such as in this case in a floating marsh in south Louisiana, crude oil comes in direct contact with plant roots and rhizomes, killing the plant. Oil degrades slowly in these anoxic wetland soils. Photographs: Irving A. Mendelssohn.*

arguably the most important determinant of severity is whether the oil penetrates the soil and comes into contact with nutrient-absorbing roots and shoot-regenerating rhizomes; this scenario can cause plant death (figure 3d). Perennial marsh plants, which regenerate new aboveground shoots each spring, usually recover from stem and leaf oiling, but oiling of belowground plant organs more often results in plant death. Although one might expect that all plant species are similarly susceptible to oil, this is not the case. Species-specific differences in responses to oil can be dramatic (Lin and Mendelssohn 1996). Oil cleanup is another important controller of oil spill impacts. Manual removal of oil by spill-response personnel can break plant shoots, which may do more harm to the vegetation than the oil itself, or they may push oil farther into the soil (Hoff et al. 1993, Hester and Mendelssohn 2000). Therefore, first responders to oil spills try to minimize such damaging impacts.

The extent of recovery of marsh vegetation after an acute oil spill impact can be just as variable as the initial effect of the spill on vegetation. In situations in which the oil has an impact only on aboveground shoots and leaves, recovery can be relatively rapid, occurring the following growing season or earlier, depending on the presence of viable propagules, the prevalence of residual oil, the extent of shoreline erosion, and the impacts of the cleanup (Hester and Mendelssohn 2000). However, when oil penetrates the soil and the initial mortality of the vegetation is extensive, recovery to reference conditions may take 3–4 years (Hester and Mendelssohn 2000) or even longer (Bergen et al. 2000, Michel et al. 2009). In extreme cases, recovery may never occur if certain intrusive remediation actions are performed (e.g., soil removal, as in the *Amoco Cadiz* spill; Baca et al. 1987, Gilfillan et al. 1995), or if erosion due to wave energy or subsidence is accelerated after plant mortality. In contrast, some remediation actions, such as *in situ* burning, can provide postspill conditions that enable initial recovery within days or weeks (Baustian et al. 2010). Therefore, although a number of factors influence the degree of impact and the speed of recovery from oiling, vegetation recovery is more the rule than the exception.

Although a US government–estimated 4.9 million barrels of oil were released into the GOM during the DWH oil spill, marsh shorelines and generally not the marsh interior were primarily exposed to the weathered oil (figure 4), a situation that limited the extent of environmental damage. Nonetheless, approximately 430 miles of marsh shorelines were oiled (Zengel and Michel 2011). Of those marsh shorelines that were oiled, 41% (176 miles) were either heavily or moderately oiled (Zengel and Michel 2011). The primary marsh types affected were salt marshes dominated by *Spartina alterniflora* and *Juncus roemerianus*; mangroves, dominated by the black mangrove (*Avicennia germinans*), which were located on small islands and shorelines and as scattered stands within salt marshes; and low- to intermediate-salinity marshes, dominated by *Phragmites australis*, the common reed, along the margin of the Mississippi River Birdfoot Delta (*http://gomex.erma.noaa.gov/erma*). Although few quantitative data are yet available on the extent of vegetation impacts throughout the oil-affected areas of the northern GOM (Mishra et al. 2012), recent findings for the salt marshes in the Bay Jimmy area of northern Barataria Bay, Louisiana documented variable impacts depending on oiling intensity (Lin and Mendelssohn 2012). Along heavily oiled shorelines (figure 5), near-complete mortality of the two dominant species, *S. alterniflora* and *J. roemerianus*, occurred. In contrast, moderate oiling had no significant effect on *Spartina*, despite significantly lowering live aboveground biomass and stem density of *Juncus*. Since the spill, some recovery has been noted for oiled marshes (Mendelssohn et al. 2011). For example, in the oiled delta marshes at the mouth of the Mississippi River, *P. australis* produced new shoots from oiled nodes on the stems (figure 6a), and *S. alterniflora* regenerated from rhizomes along moderately and some heavily oiled shorelines throughout Louisiana (figure 6b). However, as of the fall of 2011, many of the most heavily oiled shorelines had minimal to no recovery, and only time will tell whether these shorelines will revegetate naturally before shoreline erosion occurs.

The unseen responses of the benthic biota: Links to higher trophic levels

Although injury to the vegetated aboveground habitat is often the most visible impact, the effects of oil spills on benthic organisms may be especially important because of the multiple ecological processes and ecosystem functions that these organisms support. The primary productivity of benthic microalgae may rival that of macrophytes, and benthic microalgae serve as the principal food resource for much of the wetland food web. As ecological engineers, infauna bioturbate and aerate sediments, facilitate the decomposition of detritus, and enhance the flux of nutrients between sediments and the water column. They also serve as food for nekton (fishes and other natant organisms) foraging on flooded wetlands. Epifauna (e.g., the marsh periwinkle) may contribute to trophic cascades that regulate macrophyte abundance, and reef-building suspension feeders (mussels and oysters) create nursery habitat for many species. The biomass, species composition, and availability of benthos therefore affect higher trophic levels in food webs that include humans, and they even contribute to the persistence of wetlands.

Oil spill impacts on benthos can be variable and therefore difficult to predict. The toxic effects of oil can cause an acute reduction in the abundance of benthic invertebrates due to mortality or avoidance (Sanders et al. 1980), although minor or subtle changes in abundance have also been documented (Lee et al. 1981, DeLaune et al. 1984). Differences in responses are likely due to many of the same factors discussed for marsh vegetation. For benthic fauna, the indirect effects of oil on oxygen availability may also be especially significant. If high rates of mortality occur, opportunist species colonize and reach high population densities.

Figure 4. Although the* Deepwater Horizon *spill caused extensive oiling of marsh shorelines, the oil did not generally penetrate into the vast interior of these marshes (29 July 2010). Photograph: Irving A. Mendelssohn.

These disturbance specialists are typified by small-bodied, deposit-feeding annelids, such as *Capitella* species. Wetlands that have been chronically exposed to low-level hydrocarbon contamination may have communities that are relatively resistant to oil spills (Carman et al. 2000a). Toxicity is also influenced strongly by the chemical composition of the oil, as was discussed previously, and by the presence of other stressors, such as metals or high nutrient concentrations (Sundbäck et al. 2010).

Even if an oil spill does not cause a large reduction in abundance, the relative abundances of benthic species typically change, increasing or decreasing after exposure to hydrocarbons (Carman et al. 1997). Although the broader impacts of such changes in species composition are not well understood, an increasing body of literature indicates that indirect effects can ripple through communities and ecosystems, and such effects can be more significant than those of direct oil toxicity (Fleeger et al. 2003). For example, there is substantial evidence from microcosm- and small-scale field experiments that toxic effects on benthic consumers lead to dramatic changes in the composition of benthic microalgal communities (primarily diatoms, and secondarily cyanobacteria). A reduction in the abundance of oil-sensitive consumers leads to high growth and

Figure 5. Along heavily oiled shorelines, the oil caused plant mortality, leaving an unvegetated marsh platform that can be subject to wave erosion. Vegetation recovery has thus far been minimal in the most heavily oiled seaward marsh zones (3 September 2010). Photograph: Irving A. Mendelssohn.

Figure 6. Vegetative regrowth from heavily oiled plants occurred in some marshes during and after the spill. (a) Green shoots produced from the nodes of oiled stems of* Phragmites australis *in the Mississippi River Birdfoot Delta (14 July 2010). Although the stems appeared dead (necrotic), the plants were viable and produced new shoots. (b) Green tillers produced from belowground stems (rhizomes) of heavily oiled* Spartina alterniflora *plants in northern Barataria Bay, Louisiana (3 September 2010). Photographs: Irving A. Mendelssohn.

altered species composition of benthic microalgae. These changes also lead to the formation of dense microalgal biofilms, which dramatically alter the flux of nutrients and oxygen between sediments and the overlying water (Carman et al. 2000b).

The effects of oil cleanup on benthos are also highly variable. Dispersants and oil together can have a greater impact on benthic communities than oil alone, and techniques that clip and remove macrophytes affect the benthic community much more than would an absence of such intervention in some marshes (DeLaune et al. 1984). Techniques causing additional disturbances (e.g., foot traffic) to the wetland itself may also harm the marsh benthic community. In fact, it has frequently been concluded that the best approach for benthic communities may be no cleanup at all.

The ecological services provided by benthic invertebrates in Louisiana wetlands may have experienced a broad range of effects from the DWH spill, and these effects probably varied, depending on many factors. Because of their high biomass and ecosystem-engineering qualities, large epifauna, such as fiddler crabs, oysters, periwinkles, and ribbed mussels, have a high potential to alter marsh ecological function. Fiddler crabs are sensitive to the toxic effects of oil, and therefore, declines in abundance could cause indirect effects that are significant but difficult to predict. The marsh periwinkle (*Littoraria irrorata*) has a significant grazing impact on *Spartina* (Silliman et al. 2005). Toxic effects on *L. irrorata* would presumably decrease grazing pressure on *Spartina* and may aid its postspill recovery. However, oil toxicity expressed on *Geukensia demissa* (the ribbed mussel) may reduce *Spartina* production, because mussels increase soil nitrogen content (Bertness 1984). Oysters are the principal benthic suspension feeder in the northern GOM and appear to be sensitive to oil—particularly to oil suspended in the water by dispersants. They may also have suffered from the effects of reduced salinity after freshwater diversions were opened to increase outflow from coastal bays in an attempt to prevent the entry of oil into marshes. Oyster reefs provide important habitat for many estuarine species, and therefore, the indirect effects of oyster toxicity could be substantial. Benthic infauna in Mississippi River Delta marshes is typically composed of small surface-deposit-feeding macrofauna (mostly small annelids) and meiofauna (mostly nematodes and copepods) (Carman et al. 1997) that are consumed in high numbers by juvenile fishes and by crustaceans, such as brown shrimp. Oil-induced changes in species composition in Louisiana will likely not greatly affect the body size of infauna, and therefore predation rates by nekton may be less affected than in other wetlands.

Potential impacts on fishery resources: The transfer to higher trophic levels

Impacts on both vegetation and benthos can translate to higher trophic levels and may impact fishery resources. Given that the spill occurred offshore of Mississippi River Delta wetlands, the focal point of the *Fertile Fisheries Crescent*, which extends east and west into Mississippi and Texas, the potential impact on fisheries is of national concern (Gunter 1963). Over 90% of coastal fishery landings in the region are derived from species using estuaries at some point in their life cycles (Gunter 1967). Most fishery species spawn in nearshore or offshore waters of the northern GOM. Species in their early life stages enter estuaries and use the shallow wetlands therein as nursery and rearing areas. Estuaries within the Mississippi River Delta provide habitat for estuary-dependent species populating coastal systems across the northern GOM.

Nektonic species may be directly exposed to oil when they swim through concentrations of dissolved or suspended petroleum constituents. Gill-breathing animals, such as fishes, exchange gases and solutes with their environment across gill surfaces. Gill damage imperils respiration, and gill uptake results in a body load of toxins that may have lethal or sublethal effects (Whitehead et al. 2011). Individual contaminants may be at low concentrations and may have only minor or sublethal effects, but the individual and combined effects of other petroleum constituents, dispersants, and other contaminants may greatly lower ecological performance and may be synergistic (Stead et al. 2005). The sublethal effects of the DWH spill on a marsh fish (*Fundulus grandis*) in northern GOM salt marshes were shown to include effects on genes, enzymes, and gills, even though tissue loads were low or undetectable (Whitehead et al. 2011); therefore, low levels of exposure can lead to large and delayed effects on individuals and modeled populations (Rose et al. 2003).

Coastal fishery populations are vulnerable to oil spills both in their spawning grounds in the GOM and in estuarine nursery areas. Eggs and individuals at early life stages are particularly susceptible to the toxic effects of petroleum hydrocarbons (Whitehead et al. 2011), and spills near vital spawning areas that coincide with spawning events may have large impacts on recruitment and, eventually, on adult populations. For example, Pacific herring spawned in Prince William Sound, Alaska, shortly after the 1989 *Exxon Valdez* oil spill. Much of the spawning habitat and all age classes of herring were exposed to oil. Although a clear link between the spill and the Pacific herring population in Prince William Sound was never established, the herring's decline was coincident with the spill, and the population has still not recovered (Thorne and Thomas 2008); however, Pearson and colleagues (2012) see the connection as unlikely.

In the case of the DWH event, the spill overlapped with peak spawning periods for several important fishery species spawning in the GOM and in coastal passes, including brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), blue crab (*Callinectes sapidus*), and spotted seatrout (*Cynoscion nebulosus*). Although the location of the spill was in deep water, currents carried oil into the shallow spawning areas of these species. The short- and long-term effects of this oil (and dispersants) on eggs and larvae are not yet known, but Fodrie and Heck (2011) did not find short-term negative impacts of the spill on juvenile fishes associated with inshore seagrass beds. Many of the species included in their study spawn offshore, where their eggs and larvae could have been exposed to DWH oil. Their comparisons of the pre- (2006–2009) and postspill (2010) abundances of newly settled juvenile fishes in seagrass beds from the Chandeleur Islands, Louisiana, to Saint Joseph Bay, Florida, revealed no losses of 2010 cohorts or shifts in the composition of the fish assemblages of seagrass beds.

The response of nekton populations to an oil spill may depend on species differences in longevity. Populations of short-lived (1–3 year) fishery species (e.g., gulf menhaden, penaeid shrimps, blue crab) are quite volatile, following good and bad years of spawning success. Additional mortality from a large oil spill could accentuate this volatility and could cause an immediate decline in the populations and fisheries of these species. If the effects of the spill are brief and if damage to essential habitats is neither extensive nor long lasting, recovery for these species can also be rapid—within 1 or 2 years (Tunnel 2011). In contrast, the effects of high-mortality years or low recruitment on a long-lived species (e.g., red drum [*Sciaenops ocellatus*]) may not be seen immediately but could leave gaps in the age structure of the population, which could affect future reproductive output.

The Mississippi River Delta's most important fishery asset is its expansive coastal wetland system, with an extensive marsh-edge shoreline that provides feeding and shelter sites for fishery and forage species in their early life history stages. This marsh-edge shoreline is also the wetland habitat most vulnerable to oiling, because shoreline vegetation is the first to come into contact with oil driven in from adjacent waterways (figures 4 and 5). Although oil from the DWH spill had undergone considerable weathering before making landfall, *F. grandis*, which is closely associated with coastal marshes of the northern GOM, showed significant sublethal effects from exposure to weathered DWH oil in the marshes of Barataria Bay, Louisiana (Whitehead et al. 2011).

Fish are mobile organisms and, therefore, may avoid heavily oiled shoreline habitat (Roth and Baltz 2009), but if this primary habitat is limited, these individuals will be forced to use less-favorable alternatives. Where oiling is less severe, hydrocarbon concentrations may be too low to be detected and avoided. For example, background levels of weathered oil in marsh sediments do not diminish the use of shoreline marsh by most estuarine organisms (Rozas et al. 2000). In some cases, fish and other animals may not avoid lightly to moderately oiled habitat, in spite of its toxicity, and the use of these areas may induce long-term chronic health (sublethal) effects (Whitehead et al. 2011). The long-term use of oiled sites and the avoidance of primary habitat may both negatively affect fishery populations. Therefore, the relative availability of unoiled shorelines, which is extensive (Zengel and Michel 2011), as alternative habitat will be an important mediator of long-term impacts.

Notwithstanding any avoidance strategy, the indirect exposure to petroleum hydrocarbons by fishery species may result from ingestion of exposed prey. Many prey taxa (e.g., annelids, meiofauna) have a high petroleum tolerance (Peterson et al. 1996, Carman et al. 2000a), and some may harbor relatively high hydrocarbon concentrations (DeLaune et al. 1984). Predators feeding on contaminated prey can accumulate an additional body load to that acquired from direct exposure. Exposure to petroleum hydrocarbons may also change the species composition of food webs (Carman et al. 2000a). Sensitive species will diminish in population size and reduce prey availability to higher trophic levels. As was noted above, the indirect effects of oiling events often spread through the food web in unforeseen ways.

Clearly, then, fishery species responses to large-scale disturbances such as the DWH spill may be difficult to tease out from the high interannual variability in the populations of most species (Rose 2000) and from a long history of human and natural perturbations and overfishing (Chesney et al. 2000, Jackson JBC et al. 2001). The responses of these populations to the 2011 Mississippi River flood may, in particular, obscure any potential spill effects. Fisheries closures, such as those implemented following the DWH spill, may also be confounded with the spill effects and may make those effects difficult to isolate (Fodrie and Heck 2011). Moreover, fish populations and recruitment are likely to exhibit compensatory responses (e.g., better growth and lower mortality of survivors) to an episodic stress or mortality event from a spill; therefore, a spill may not necessarily affect adult population numbers and biomass if the exposure is not sustained or widespread (Tunnell 2011). However, a spill during critical life stages could reduce recruitment and could add an additional stress to populations already burdened by overfishing, reduced habitat quality, and contaminants (Rose 2000). The uncertainties associated with the potential impacts of the DWH spill on fishery populations and fisheries may be greater than that for most other biotic components of the ecosystem and will probably be difficult to resolve (Tunnell 2011). A final conclusion on the assessment of spill effects may not be possible for years.

Integrating impacts through ecosystem services

The impacts of oil on the ecological structure and function of wetland ecosystems may alter the resulting benefits to human well-being, which are often referred to as *ecosystem services* (Maltby 2009). The extensive literature on the functioning of coastal wetland ecosystems both worldwide and adjacent to the GOM demonstrates the importance of healthy, functioning coastal wetlands to local, regional, and national economies. Coastal wetland functioning is underpinned by fundamental hydrogeomorphic, biogeochemical, and ecological processes that are susceptible to changes from environmental as well as human-induced perturbations. Oil spills, like the DWH event, are one such human input that can alter important ecosystem services, which are derived from ecological functions, and these inputs may have adverse consequences for the flow of benefits to society. For example, coastal marshes can act as storm barriers, providing the services of flood-risk reduction and prevention of property damage; they also promote nutrient cycling and assimilation, which helps to prevent the eutrophication of adjacent estuaries; and they provide the habitat and food-web support underpinning both commercial and recreational fisheries. Directly or indirectly, oil contamination may alter these ecosystem services.

Interest in ecosystem services has significantly gained prominence since its formalization by the United Nations Millennium Ecosystem Assessment (MA) in 2005. The MA placed ecosystem services into four categories: provisioning, regulating, supporting, and cultural (figure 1). Ecosystem services in each category contribute variously to societal well-being, economics, and culture, as well as less directly through the maintenance of environmental quality. Coastal wetlands can perform many of the services listed in figure 1 (see UK National Ecosystem Assessment 2011 for the most recent review). The formal recognition of the wide range of services and the resulting benefits provides the framework to link the condition of (and impacts on) the coastal environment with the human economy in practical terms. These can include both nonmarket and more traditionally accounted market values, as well as important metrics such as jobs and particular community values.

Research has long established links between simple ecosystem descriptors, such as coastal wetland area (which is indicative of their nursery functions) and coastal fisheries production. However, considerable uncertainty over the precise relationships among specific coastal ecosystem processes, functioning, and the quantity and quality of the resulting services still exists. This is a significant and challenging research area in which focus is necessary in order to strengthen the evidence base for a full assessment of environmental impacts such as oil spills. The disproportionate importance of the natural capital of wetlands and the adjacent coastlines to the nation's renewable resources cannot be overemphasized. For example, a recent study in the United Kingdom has revealed that although coastal habitat constitutes only 0.6% of its land area, the total value of the ecosystem services provided by it is 3.5% of gross national income, or more than $72 billion (adjusted to 2003 values; UK National Ecosystem Assessment 2011).

Of all the ecosystem services that coastal wetlands support, the two most easily quantified are arguably fishery support and production. Ports in Louisiana, Mississippi, and Alabama typically account for 90% of the commercial fisheries biomass harvested from the five US states bordering the northern GOM and for approximately 30% of the US fisheries production. In 2009, revenue from fisheries landings in the northern GOM exceeded $697 million, with more than half of that value derived from the harvest of penaeid shrimps (NMFS 2010). However, a comprehensive assessment of direct economic fisheries losses in the wake of the DWH oil spill requires the inclusion of both dockside losses and losses to seafood dealers, processors, and retailers. Moreover, economic losses to the recreational fishing sector could prove equal to or greater than commercial fisheries losses. In 2009, 6 million anglers took 22.4 million recreational fishing trips in the GOM region. The trip-related expenditures from those anglers provided more than $2 billion in revenue for fishing-related businesses (NMFS 2010). Unlike their commercial counterparts, revenues in recreational fisheries are primarily a function of human population. Correspondingly, recreational losses are expected to be greatest in spill-affected coastal regions with large angler populations. These apparent economic losses to commercial and recreational fisheries thus far are due to fishery closures, vessels leaving the fishery for spill cleanup work, and consumer perception and choice, rather than to effects on stocks. As with other spills, the full extent of the impacts of the oil, itself, on fisheries will only become apparent after some years.

Conclusions

Although more than two years have passed since the DWH blowout, considerable uncertainty still exists concerning both the short- and long-term impacts of the oil spill on wetland ecosystems (DeLaune and Wright 2011). With the exception of the obvious impacts on shoreline marsh vegetation, the short-term effects on microbial communities, benthic and epibenthic biota, and marsh-dependent fishes and fisheries are still being investigated. Few published studies specifically identifying impacts on the wetlands from the DWH spill are available at this time. Furthermore, information on the impacts on wetland biogeochemical processes and the resulting ecosystem services together with their ultimate link to human well-being is absent. Investigations being done through the Natural Resource Damage Assessment and by independent scientists will certainly fill in some of these gaps over time. Regardless, the long-term impacts will be even more difficult to quantify. This is especially relevant to the Mississippi River Delta ecosystem, where wetland degradation has been a chronic problem due to a variety of natural and human-induced factors, such as the leveeing of the Mississippi River and dam construction upriver, the river's present fixed position, land subsidence from oil and gas extraction and natural geologic processes, extreme weather conditions such as hurricanes and droughts, invasive species (e.g., the nutria), and canal construction for oil and gas activities and for navigation. These impacts caused a 5400-square-kilometer loss of wetlands between 1930 and 2010 (Couvillion et al. 2011), the greatest wetland loss in the United States. Whether the DWH event has accelerated this loss is presently unknown.

A major concern relative to wetlands is whether their sustainability and resistance to future disturbances have been degraded by the DWH spill. The Mississippi River Delta wetlands remain viable only if their rate of elevation change keeps pace with the rate of relative sea-level rise (a result of both land subsidence and global sea-level rise). In addition, marsh shorelines that have become unvegetated because of oil impacts may experience increased shoreline erosion, which may contribute to wetland loss. Similar to those of the *Exxon Valdez* oil spill, the impacts on coastal ecosystems, including wetlands, from the DWH spill may not be immediately evident and will require future evaluations to enable us to more fully understand the spill's ecological consequences. Given that the wetlands associated with the Mississippi River Delta system were in a state of deterioration prior to the DWH event, it will be all the more difficult to differentiate between future impacts caused by the DWH event and those resulting from the ongoing processes of wetland degradation (Boesch et al. 1994). This problem of separating DWH oil-related impacts from the multitude of other perturbations to the Mississippi River Delta ecosystem will be the ultimate challenge for scientists and resource managers attempting to accurately assess long-term injury from the spill.

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