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Effects of the Deepwater Horizon Oil Spill on Coastal Marshes and Associated Organisms

By Nancy N. Rabalais and R. Eugene Turner



Photo credit: R.E. Turner

ABSTRACT. Oil gushed from the Macondo Mississippi Canyon 252 well into the Gulf of Mexico for 87 days after the Deepwater Horizon drilling rig exploded and sank. A concern, after widespread dispersant use offshore on surface waters and at the wellhead, was that the oil/dispersant mixture would reach valuable, and vulnerable, coastal ecosystems. Standardized oil spill response methodology identified 1,773 km of the 7,058 km of surveyed shoreline as oiled, with 1,075 km oiled in Louisiana. This paper synthesizes key results of published research on the oiling effects on coastal habitats and their inhabitants from microbes to vertebrates. There were immediate negative impacts in the moderately to heavily oiled marshes, and on the resident fish and invertebrates. Recovery occurred in many areas within the two years following the oiling and continues, but permanent damage from heavily oiled marshes resulted in eroded shorelines. Organisms, including microbial communities, invertebrates, and vertebrates, were diminished by acute and chronic hydrocarbon exposure. However, the inherent variability in populations and levels of exposure, compounded with multiple stressors, often masked what were expected, predictable impacts. The effects are expected to continue to some degree with legacy hydrocarbons, or the marsh ecosystem will reach a new baseline condition in heavily damaged areas.

INTRODUCTION

The sequence of events for the Deepwater Horizon oil spill began April 20–22, 2010, when the drilling rig exploded and collapsed to the seafloor 1,500 m below. Oil from the ruptured wellhead spewed a collective 5 million barrels (210 million gallons) of Macondo Mississippi Canyon block 252 oil over the 87 days before the wellhead was capped on July 15, 2010 (McNutt et al., 2011). Concerns about the oil reaching valuable and vulnerable shorelines in the northern Gulf of Mexico (GoM) prompted the federal Unified Command to approve the use of dispersants, both on the water surface and at the wellhead, in order to limit the amount of oil reaching the shore. Brownish oil/dispersant emulsions (often called mousse), oil droplets, tar balls, and surface sheens began reaching shorelines in May 2010 and peaked in June 2010. The oiling of beaches, salt marshes, mangrove stands, seagrass meadows, and estuarine waters continued well after July 15, 2010, following the capping of the Macondo well. The wellhead was officially declared shut in on September 19, 2010.

The level of shoreline oiling was determined from the standard Shoreline Cleanup Assessment Technique (SCAT; ERMA, 2015). The SCAT analysis identified 1,773 km of 7,058 km of oiled shoreline surveyed in the first year (heavy to trace; Michel et al., 2013). The majority of all oiled shorelines and most marsh oiling were in Louisiana (>60% and 95%, respectively; Michel et al., 2013). Nixon et al. (2016) updated the 2015 SCAT analysis and added 2,113 km (out of 9,545 km surveyed) to the oiled shoreline inventory, representing a 19% increase in oiled shoreline. The Deepwater Horizon oil spill represents the largest oil spill in history as measured by shoreline length.

Many of the oiled areas exhibited some form of hydrocarbon contamination for many years. There were tar balls on sandy beaches already, and the interior waters and sediments had a baseline concentration of petroleum hydrocarbons from leaks, pipeline breaks, and diesel-supported marine transportation after years of coastal oil and gas production that began in the early 1940s, and, until 1997, also included oil and gas production

wastes (National Research Council, 2002; Veil et al., 2004; Theriot, 2012). Assessing the effects of the Deepwater Horizon oil spill on coastal habitats is difficult because of these legacy effects and other confounding factors, including, for example:

1. Inadequate background data
2. Uneven initial oiling, horizontal and vertical redistribution of oil, and oil degradation
3. A sparsely known background of “oil exposure” within coastal landscapes
4. Complicated and interactive marsh processes and food webs
5. Additional stressors, for example, salinity gradients, marsh elevation, drought, flooding, eroding landscapes, and storms
6. The mismatch of negative impacts at genomic and physiological levels on individuals compared to an absence of measurable impacts among populations and communities in field studies
7. Unprepared but necessary level of large-scale science infrastructure to respond to the event

Further, the “levels” of impact vary by, for example, location, time, and toxicity, and longer-term effects may not yet be fully recognized or manifested.

Some background data were available from “Early Response” grants funded by BP and from the National Science Foundation Rapid Response Research (RAPID) program. These programs, and others, provided for data collection before the oil’s landfall and immediately afterward. More fully funded studies that began after the oil spill, such as the Gulf of Mexico Research Initiative and the required Natural Resource Damage Assessment, provided opportunities to follow effects for longer periods, now six years in some cases. The results presented here are from the published literature and are mostly related to salt marshes.

OIL DISTRIBUTION AND DEGRADATION

Shorelines with “heavy” to “moderate” oiling were located mostly in southeastern Louisiana (Figures 1 and 2). The marsh oiling was initially heterogeneous in space, time, and amount, as well as later in re-oiling and degradation (Overton, 2016, in this issue). This provided many opportunities to establish pre- and post-spill sites, and “reference” sites for observations, measurements, determination of

change (if any), and mitigation success. The Macondo oil was visually evident at the marsh edge and for at least 100 m inland (Ramsey et al., 2014; Turner et al., 2014b; Figure 3). The average concentration of total alkanes and polycyclic aromatic hydrocarbons (PAHs) in southeastern Louisiana marshes in June 2013 was 20 times and 374 times the pre-oiled conditions, respectively (Turner et al., 2014a; Figure 4). Although the concentrations of total alkanes in June 2013

were on a trajectory to be near baseline levels by 2015, this did not occur, and the concentration of PAHs may take many decades to reach original baseline levels—or establish new baseline levels. The concentrations of alkanes and aromatics were not at pre-spill levels in 2015. Multiple resuspension events and high water from tropical storms and hurricanes through November 2013 redistributed oil-contaminated sediments (Figure 3; see also Overton et al., 2016,

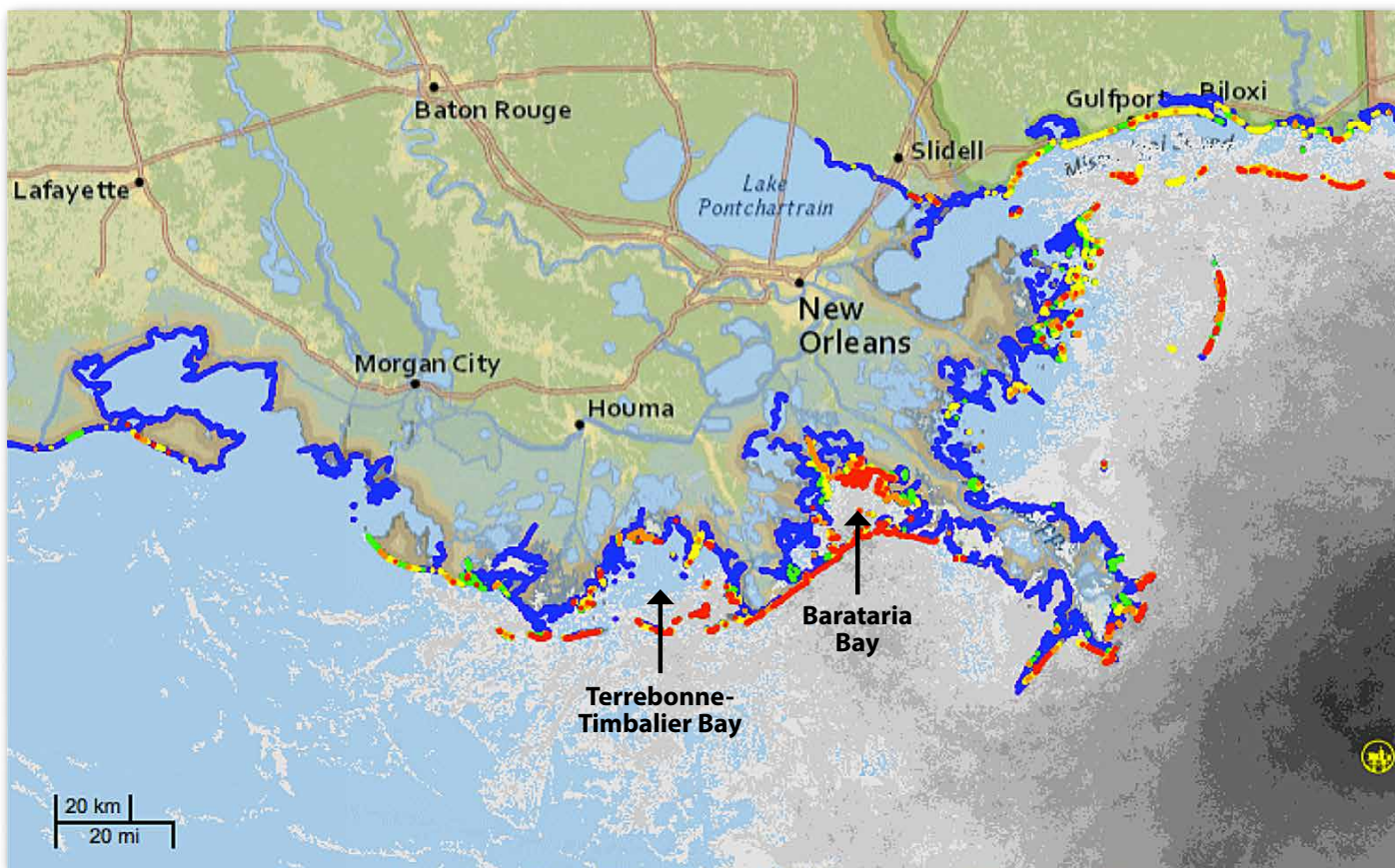


FIGURE 1 (above). This Shoreline Cleanup Assessment Technique (SCAT) map documents the level of oiling along the Louisiana-Mississippi shoreline from May 2010 to May 2012. The red and dark orange dots represent heavy and moderate oiling, respectively, especially in southeastern Louisiana. The location of the Macondo wellhead is in the lower right corner. Data are available at: <http://gomex.erma.noaa.gov>.

FIGURE 2 (right). Heavily oiled shoreline in Bastian Bay (eastern Barataria estuary), September 6, 2010. *Photo credit: R.E. Turner*



in this issue, who discuss remnants of the remaining less-degraded oil in 2015, which was probably sequestered inside fiddler crab burrows).

SALT MARSHES

Public perception is that oil spills are detrimental to marshes and their ecosystem services, such as nursery habitat, materials recycling, and diminution of storm surge. What may appear to be “normal” marshes may be obscured by unapparent impacts that define marsh health. It is also difficult to “see” an impact on an oiled marsh if the marsh has eroded away.

Marsh Health

Early assessments (Lin and Mendelssohn, 2012; Silliman et al., 2012; Zengel et al., 2015) clearly documented the dieback of all marsh vegetation in heavily oiled areas in July 2010. The typical response was the absence of living vegetation and the presence of dead stems layering the exposed, oiled sediments. Various reassessments were made after six to 24 months for vegetation health and shoreline erosion (see below).

Vegetation cover after seven and 16 months (Silliman et al., 2012; Lin and Mendelssohn, 2012, respectively) remained much lower than in the control sites, but sparse vegetation recovery after two years, as identified by Zengel et al. (2015) differed considerably from the results of Silliman et al. (2012), who reported “recovered” vegetation in three control versus three heavily oiled plots 17 and 20 months after oiling. The Zengel et al. (2015) study benefited from greater replication, a longer-time series, and the placement of all treated (including no treatment) plots within the same 11 km of shoreline and reference plots within 3 km of treatments, thus minimizing multiple aspects of environmental variability.

Juncus roemerianus (black needlerush) and *Spartina alterniflora* (smooth cordgrass) are two dominant plant taxa in many southeastern Louisiana marshes. Lin and Mendelssohn (2012) followed several indicators of marsh plant “health” in these two species seven months after Macondo oil landfall in “heavily” or “moderately” oiled areas in the same Barataria Bay estuary as Silliman et al. (2012) and Zengel et al. (2015). The total PAH averaged 510 mg g dry soil⁻¹ in the upper 2 cm of heavily oiled marsh, was <100 mg g dry soil⁻¹ in moderately oiled marsh, and was “minimal” in reference marsh sediments (<10 mg g dry soil⁻¹). The average live aboveground biomass of both species combined was significantly lower, almost none, in the heavily oiled marsh compared to the reference marsh, but there was no significant difference between the combined weight of the two species in the moderately oiled marsh and the reference marsh. The live *S. alterniflora* aboveground biomass and stem density was about 10 times greater than for *J. roemerianus* in the moderately oiled marsh. If the aboveground live biomass were a predictor of recovery, then one might predict a faster recovery of *S. alterniflora*

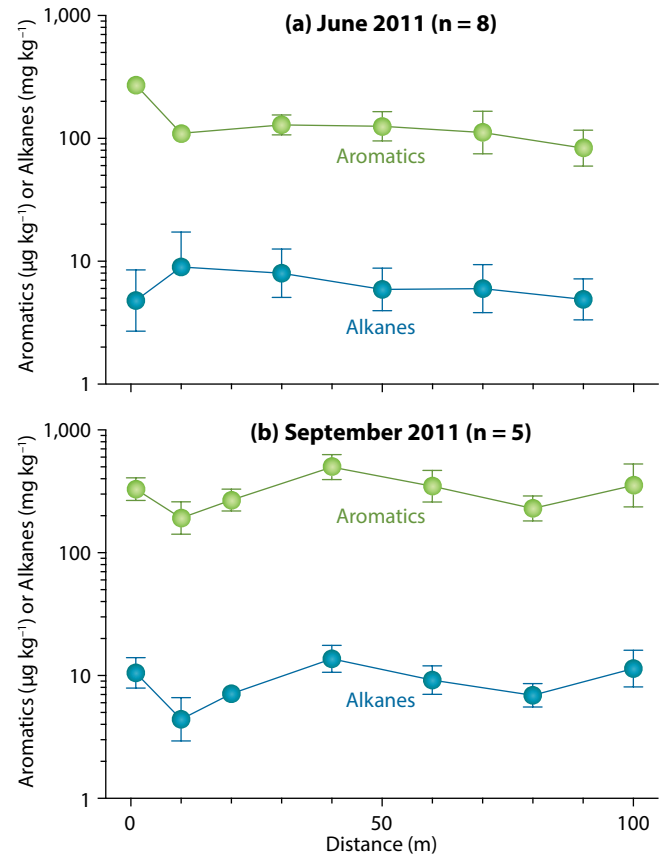


FIGURE 3. The concentration ($\mu \pm$ SE) of target alkanes (mg kg^{-1}) and polycyclic aromatic hydrocarbons (aromatics) along (a) eight 90 m transects in Barataria Bay in June 2011, and (b) five 100 m transects in September 2011. Distance is from the marsh edge existing at time of sampling. From Turner et al. (2014b)

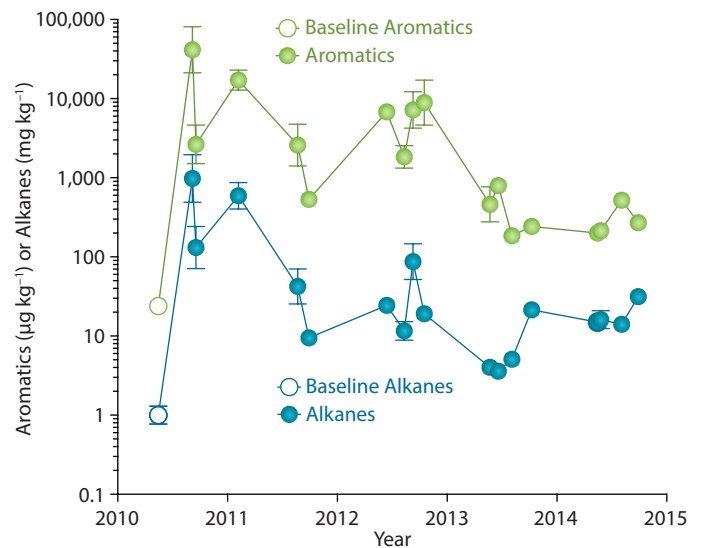


FIGURE 4. Trajectory of change in hydrocarbon components generated and updated with data from Turner et al. (2014a).

than of *J. roemerianus*. A parallel greenhouse mesocosm experiment following similar attributes but with differential oiling indicated that *J. roemerianus* did not fare as well as *S. alterniflora* as was the case in the oiled in situ marshes (Lin and Mendelsshon, 2012). These authors and others (Lin et al., 2016) followed marsh recovery up to 42 months after the spill, and near-complete plant mortality remained the case for heavily oiled marshes, and live aboveground biomass was only 50% of that in the reference marshes by then. Shoreline marshes with mixed *Spartina-Juncus* communities shifted to a predominant *Spartina* marsh after two to three years, further supporting results from seven months (Lin and Mendelsshon, 2012). Although belowground indicators of marsh health were not a focus of the Lin and Mendelsshon (2012) study, Lin et al. (2016) recorded loss of belowground vegetation and reduced soil shear strength similar to that seen by McClenachan et al. (2013).

The responses of marsh vegetation to experimental cleanup treatments were followed by Zengel et al. (2015) to better inform future oil spill mitigation efforts. The treatments were “none,” manual removal by crews scraping vegetation with hand tools, mechanical removal of oiled plants, mechanical raking, cutting and scraping of plants and soil, and nearby unoiled reference areas. An additional experiment involved planting

Spartina alterniflora stems in mechanically cleaned areas. The average total PAH concentrations ($\sim 130 \text{ mg kg}^{-1}$) were two orders of magnitude higher in the oiled than in the reference marsh. Manual treatment resulted in greater vegetation cover than mechanical treatment and untreated marshes, at least through one year (Figure 5). All the heavily oiled plots showed some increases in vegetation cover with time, whether treated or untreated; however, reference marshes had a much higher percent vegetation cover than either treated or untreated marshes for more than two years after the initial oiling. The planting experiments demonstrated that vegetation recovery was quicker with planting than with no planting and that shoreline retreat was reduced where there was planting.

Marsh Biogeochemical Processes

Changes in vegetation cover, above- and belowground living biomass, and community diversity and productivity were visible outcomes from the oiling of salt marshes, but nutrient and carbon cycling were also predicted to be altered by the presence of oil on the marsh plants and in marsh sediments, either settled on the sediment surface or mixed in with processes of resuspension and subsequent accumulation.

The mediators of biogeochemical processes in marsh soils are the microbial communities, which often provide

more of an indication of shift in processes and cycling of materials than direct measures of nutrient cycling rates (Bernhard et al., 2016). Ammonia-oxidizing archaeal (AOA) and bacterial (AOB) communities varied across three research sites in Terrebonne Bay, central Barataria Bay, and eastern Barataria Bay, but not according to differences between “oiled” and “unoiled” transects within each area (Marton et al., 2015). Similar to nitrogen cycling processes, the phosphorus (P) sorption potential index differed across the three areas studied by Marton and Roberts (2014) and Bernhard et al. (2016) and within a site, but did not differ between the “oiled” and “unoiled” marshes. The results suggested that the mineral composition of marsh soils, influenced by elevation-inundation gradients, was critical in dictating P loading to estuaries and open waters, and overall marsh functioning. Further, within two years of the Deepwater Horizon oil spill, the oiled marshes were able to adsorb phosphorus at levels comparable to unoiled marshes.

The diversity of the microbial community was significantly lower with increasing total petroleum hydrocarbon (TPH) concentrations in the top 2 cm of sediments, dropping from a Shannon diversity index of 5 to 1.5 when TPH concentrations increased from $10,000 \text{ mg kg}^{-1}$ to $100,000\text{--}500,000 \text{ mg kg}^{-1}$ (Atlas et al., 2015). The microbial community diversity increased over time as the diversity of the microbial community approached that of unoiled reference sites in Bay Jimmy (upper and eastern Barataria Bay, Louisiana; Atlas et al., 2015). As oil concentrations decreased over time, microbial diversity increased and approached the diversity levels of the reference sites, at least in the top 2 cm of sediment cores.

Marsh Erosion

Shoreline retreat (= erosion) is a significant factor in “recovery” because emergent vegetation seldom reestablished after oiling (McClenachan et al., 2013; Turner et al., 2016). Several research groups identified the rates of erosion

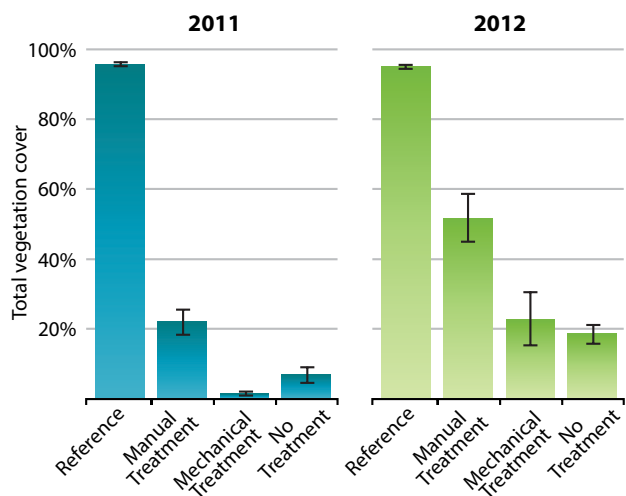


FIGURE 5. Total vegetation cover in 2011 and 2012. Differences among oiling/treatment classes, years, and the interaction of oiling/treatment class and year were observed (all $p < 0.01$). Data are means ± 1 SE. $N = 9$ for the heavily oiled plots with no treatment; $n = 5$ for all other oiling/treatment classes including reference. From Zengel et al. (2015)

(Silliman et al., 2012; McClenachan et al., 2013; Zengel et al., 2015), and others noticed shoreline erosion while conducting field studies (Turner et al., 2016). The marsh loss from oiling is additive to the negative effects of other human and natural processes contributing to coastal erosion (42.9 km² yr⁻¹ from 1985 to 2010) (Couvillion et al., 2011).

McClenachan et al. (2013) identified 30 sites along a shoreline that ranged from “low” oil (<200 g kg⁻¹ PAHs; most without the Macondo oil chemical signature) to “high” oil (>20,000 µg kg⁻¹, all with the Macondo oil chemical signature). The measurements began in November 2010 and included shoreline erosion, soil strength, percent vegetation cover, sediment PAH concentrations, and marsh overhang (distance from marsh edge

where sediments beneath the root mat had eroded away). They may have missed some initial high erosion rates at heavily oiled sites because of the initial toxic effect that tripled erosion rates on islands (Turner et al., 2016) and shorelines (Hester et al., 2016). The marsh overhang for the high oil sites was significantly greater than for the low oil sites, with the exception of one sample (Figure 6). Further, soil shear strength was similar in the upper 50 cm of both high- and low-oil sites, but the shear strength was much lower below 60 cm in the high oil sites than in those with low oil (Figure 6). There were no significant differences in the percent *S. alterniflora* vegetation cover for four of five sampling periods. After then, the erosion increased at the low oil sites as the promontories created by erosion of adjacent oiled

sites left them exposed to wave action. McClenachan et al. (2013) make the case for longer-term studies, non-reliance on some standard marsh “health” indicators, and additional measurements that might identify important processes.

RESPONSE OF MARSH ORGANISMS

Several marsh organisms play a key role in marsh community structure and are potential bio-indicators in intertidal marsh habitats—blue crabs, fiddler crabs, periwinkles, mussels, and oysters. Blue crabs, like marsh nekton, are highly mobile, and, thus, exposure might be difficult to predict. The exposure for attached organisms, for example, mussels and oysters, can be determined from intertidal waters and sediments. Suitable organisms to follow before, during, and after an oil spill are fiddler crabs living in burrows that may have been flooded with oil or that eat detritus from potentially oiled sediment surfaces (Figure 7), and periwinkles that graze on epiphytes attached to live or decaying *Spartina* leaves, or on detritus. All are important marsh organisms that structure habitat, influence biogeochemical cycles, and provide integral components of food webs.

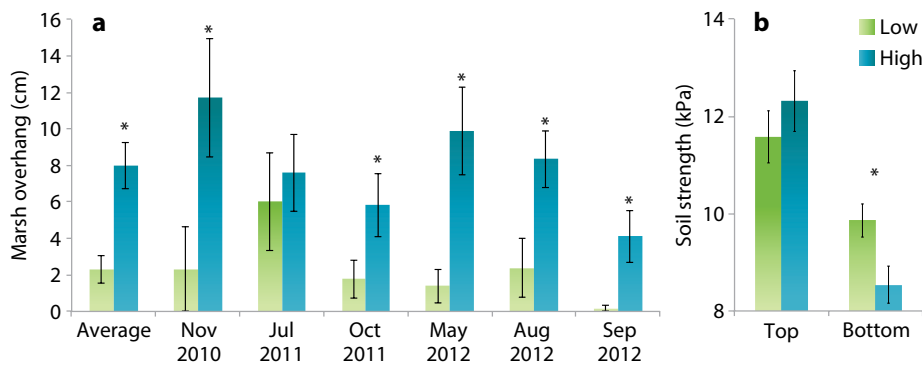


FIGURE 6 (above). (a) Overhang of the marsh (cm) for each time period in high and low oil sites. (b) Soil strength in the top layer (0–50 cm) and bottom layer (60–100 cm) of high and low oil sites in November 2010. (Both) The error bars are ±1 SE. Asterisks indicate significant difference ($p < 0.05$). From McClenachan et al. (2013)

FIGURE 7 (right). Fiddler crabs in Louisiana marsh, June 2012. Photo Credit: CWC Consortium, LUMCON



Marsh Invertebrates

Zengel et al. (2016b) conducted a five-year study of fiddler crabs (*Uca* spp.) and the effects of different cleanup methods used for heavily oiled marshes. The treatments and reference marshes were the same as in Zengel et al. (2015). They found that crab burrow abundance and diameter (as an indicator of crab size) declined, and that shifts in the proportion of two fiddler crab species occurred following oiling. A return to the “reference” abundances (reduced by 39% following oil exposure) was not complete by 2014. The burrow diameter returned to pre-spill size by 2012. They focused on *Uca longisignalis* and *Uca spinicarpa*, which usually live in less-vegetated areas with clay soils. The abundance of *U. longisignalis* declined, with a parallel increase in the proportional composition of *U. spinicarpa*. Return to reference species composition will likely rely on the re-vegetation of *S. alterniflora* in damaged areas.

Zengel et al. (2016a) conducted a similar study on the marsh periwinkle (*Littoraria irrorata*). They targeted snails >6 mm length, because this size would be visible in more cryptic environments, for example, between the leaf sheath and the *Spartina* stem. A result confounding their analysis was the habitat “destruction” that resulted from raking and removing oiled plants that were the primary habitat of the periwinkles, planting of *Spartina* as one of the treatments, and the length of time required for *Spartina* habitat recovery. Still, the overall results indicate significant losses of periwinkles in oiled habitat that normally supports high snail abundances and also a continuing slow recovery in snail abundance and size distribution that was related to habitat recovery. Zengel et al. (2016a) predicted that snail population recovery will take several years and will depend on oil levels and recovered habitat conditions.

Many smaller organisms that live within the sediments of marshes are good indicators of pollution impacts because they are relatively immobile and display a range of tolerance for toxic compounds.

Fleeger et al. (2015) followed the fate of microalgae and meiofauna on the same or similar plots examined for vegetation response as Lin and Mendelssohn (2012) and Zengel et al. (2015) for up to 48 months. Meiofauna feed on benthic microalgae and themselves serve as prey to larger organisms. The meiofauna were severely damaged along with *S. alterniflora* in heavily oiled areas where TPH concentrations ranged from 50 TPH g⁻¹ to 500 mg TPH g⁻¹ sediment compared to reference marsh levels of ~0.3 TPH g⁻¹ sediment. Meiofauna recovery followed the time courses of *Spartina* recovery and TPH degradation, with substantial recovery of many organisms within 36 months of the spill, while polychaetes, ostracods, and kinorhynchans had still not recovered to background levels in reference marshes 48 months after the spill.

Filter Feeders

The eastern oyster (*Crassostrea virginica*) is an important harvestable food resource. It also provides ecosystem services in the form of oyster reef habitat for other organisms, water quality improvements through filtration, storm wave surge reduction, and effective take up of accumulated hydrocarbon compounds. La Peyre et al. (2014) studied a series of physiological responses of wild-collected or hatchery-spawned oysters to oil exposure at post-spill unoiled and oiled sites. While responses to stressors ranged from cellular to whole organism levels across and among the sites, none were related to exposure to petroleum hydrocarbons; rather, the stressors most affecting the oysters were salinity, temperature, and parasitism by the flagellated protozoan *Perkinsus marinus*. In particular, oysters collected from Breton Sound were most likely affected by lowered salinities related to the release of water through the Caernarvon freshwater diversion at Mississippi River Mile 82 upstream and also 15 miles below New Orleans as a management response to the Macondo oil spill. This diversion of freshwater into the marshes east of the Mississippi

River drained into Breton Sound. Soniat et al. (2011) documented a similar lack of hydrocarbon indicator results along a similar salinity gradient six months after the oil spill.

Carmichael et al. (2012) compared the carbon and nitrogen stable isotopes of the growing edge of an oyster shell with local suspended particulate matter to study whether oysters incorporated oil into their diets. The oysters were obtained from hatchery stock and deployed in estuarine waters of Mississippi and Alabama (1) before any oil was observed to be moving onshore, (2) when visible oil was reported from the same waters, and (3) approximately three months after oil was reported in coastal waters. The stable carbon and nitrogen isotopes in the rapidly growing oyster shells did not indicate a carbon source with an oil signature (Carmichael et al., 2012); however, the level of exposure in concentration or time was not known. Other filter-feeding organisms, such as mussels and barnacles, in oiled intertidal habitats were also examined for indications of uptake of the stable carbon isotopes reflecting oil origins and of ¹⁴C for oil age (Fry and Anderson, 2014). Oil incorporation into the diet was <1% and near detection limits. These results paralleled those of Carmichael et al. (2012) and La Peyre et al. (2014).

Marsh Insects

Husseneder et al. (2016) followed populations of the horse fly (a top predator insect in marsh food webs) biweekly in oiled and unaffected locations from immediately after the oil spill in June 2010 until October 2011. The abundance of horse flies crashed in oiled areas. The genetic studies of oiled and unoiled populations indicated that six of seven oiled populations had few breeding parents, reduced effective population size, a lower number of family clusters, and fewer migrants among populations. The beauty of Husseneder et al.’s experimental design is that it ranged from genetics to population levels on a keystone insect species with consistent oiled and unoiled results.

McCall and Pennings (2012) studied marsh arthropods during the same period as Husseneder et al.'s (2016) fieldwork. The terrestrial arthropod community in oiled and unoiled *Spartina* marsh transects was suppressed by 50% at oiled sites in 2010, but had largely recovered in 2011. Subguilds of predators, sucking herbivores, stem-boring herbivores, parasitoids, and detritivores all tended to be suppressed at oiled sites by 25% to 50% in 2010 and recovered by 2011. While the authors were cautious in extrapolating a one-year recovery of insect abundances to the health of the marsh ecosystem, they noted few differences in the vegetation in the two comparative marshes. However, measures of “dead” versus “live” marsh was quantified as a presence/absence, and the beginning of the transect was always one to two feet (0.3–0.6 m) behind the edge of healthy *Spartina*, and thus behind areas of oil-damaged vegetation.

Feathers and Fur

Early in the research programs, Bergeon Burns et al. (2014) reported on preliminary work with marsh vertebrates, especially the seaside sparrow (*Ammodramus maritimus*) and the marsh rice rat (*Oryzomys palustris*). The seaside sparrow is by far the numerically dominant bird species. Marsh rice rats are not restricted to salt marshes, but are exceptional among mammals in their abundance in coastal Gulf of Mexico salt marshes. The exposure to oil could be direct for seaside sparrows, for example, perching on oiled *S. alterniflora* stems or on stems directly above heavily oiled sediments, feeding on oil-covered sediments, and eating insect prey exposed to the oil. The marsh rat spends much time in contact with oiled sediment surfaces. The exposure level or mechanisms remain unknown, but replicating studies in oiled and unoiled were, again, based on the results of the SCAT analyses.

The level of PAHs in tissues or body fluids do not often reflect oil exposure, but the various isoforms of the gene cytochrome P450, family 1, subfamily A (CYP1A) or

CYP-related enzymes (e.g., ethoxyresorufin-O-deethylase) that are unregulated in the presence of PAHs are often used as indirect biomarkers of crude oil, PAH exposure (e.g., Head and Kennedy 2007), and adverse health effects. Preliminary seaside sparrow nesting data from 2012 and 2013 (two and three years post marsh oiling) indicate that nests on unoiled sites were significantly more

likely to fledge than those on oiled sites (Bergeon Burns et al., 2014). These preliminary and potential effects may not represent longer-term population effects in salt marsh ecosystems.

Common loons (*Gavia immer*) overwinter in coastal areas of the Gulf of Mexico. The birds are piscivorous and exposed to potential contaminants in the water or in their fish prey. Paruk et al. (2016) studied PAH levels and physiological measures in loons for five winters following the oil spill. They predicted that PAH levels in loon blood would peak following the spill and then decline, but this was not the case. The frequency of loons with PAHs and the concentration and types of PAHs varied by year, and not by an expected decline in exposure. There was, however, a strong reduction in body mass with increasing PAH concentrations in their blood—a sublethal indicator of overwintering health or future reproductive success.

Marsh and Seagrass Nekton

The research community was expecting to be able to follow the effects of Macondo oil on resident marsh nekton,

primarily those known as killifish, mosquito fish, and mummichogs. Early investigations within the first four months of marsh oiling by Whitehead et al. (2012) identified linkages between oil exposure and the genomic expression and gill immunohistochemistry, despite low concentrations of Macondo hydrocarbons in water and tissues. They suggested that heavily weathered crude oil from the spill

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imparted significant biological impacts to the fish, some of which remained for over two months following initial exposures. These expressions indicate significant genetic impacts on Louisiana salt marsh nekton that were exposed to heavy to light Macondo oiling, but expressions of the genetic abnormalities were not apparent in field studies of marsh and seagrass nekton populations. Several groups of investigators, assuming transfer of genetic, physiological, and reproductive penalties, examined in situ marsh and seagrass nekton populations for the effects of exposure to Macondo oil (Fodrie and Heck, 2011; Fodrie et al., 2014; Able et al., 2015). The mostly consistent results showed little evidence of any influence from potential Macondo oil exposure.

Able et al. (2015) and Fodrie et al. (2014) examined resident marsh killifish in oiled and unoiled Louisiana marshes in 2012 and 2013. The dominant fish were *Fundulus grandis* and *F. xenicus*, with several other *Fundulus* spp., *Cyprinodon variegatus*, and *Poecilia latipinna*. Fish were segregated into microhabitats (e.g., marsh edge, pond, creek), but there were no total nekton- or species-specific

differences between oiled and unoled subhabitats, and no overall total difference in all fish nekton between the oiled and unoled sites. Fodrie and Heck (2011) focused on seagrass beds from the Chandeleur Islands, Louisiana, to St. Joseph's Bay, Florida (all along oiled shorelines). They collected trawl samples in June–September from 2006 through 2010. There were no statistical differences among the four pre-spill years and the year of the spill for total fishes caught and across geographic areas. In an interesting analysis of levels of risk exposures of eggs and larvae to conditions that might affect successful recruitment following the spill, they found that there were no overall differences among areas in a ratio of catch-per-unit-effort (CPUE) between one year post-spill to four years pre-spill. The Chandeleur Island grouping, however, appeared to have a significantly lower ratio (i.e., a loss of CPUE) in the moderate and high exposure level. Other analyses of effects on fishing pressure with regard to post-spill versus pre-spill indicated no significant differences among the geographic areas (Fodrie and Heck, 2011; Moody et al., 2013).

A review of responses of estuarine fish community composition and measures of abundance and biomass indicate an absence of measurable impacts on populations (Fodrie et al., 2014; Abel et al., 2015). This leaves scientists with an apparent knowledge gap between laboratory oil toxicity observations (Pilcher et al., 2014) and the in situ observations by Whitehead et al. (2012) regarding genome, physiology, and reproductive disruption in freshly oiled habitats within two to four months of the peak oiling. There are multiple reasons for these apparently disparate results, including: (1) Whitehead et al.'s (2012) observations occurred over the two to four months of peak oiling, while field observations started seven months after the spill, when oil degradation was underway. (2) Initial field observations may not have been optimally timed to discern the effects on the marsh organisms' life cycles. The

seasonal effects were sometimes diminished in data groupings and comparisons made by year, rather than perhaps by a species-specific life history event. (3) Some species could move away from harmful habitats. Likewise, transient species may provide adequate recruitment. (4) Oil distribution during peak exposure and oil component concentration was quite variable over time. (5) Offshore and inshore fishery closures may have affected marsh nekton recruitment. (6) Finally, there may be a tolerance and/or adaptation to the low but chronic levels of petroleum hydrocarbons in the oil and gas production fields in coastal Louisiana.

CONCLUSIONS

Heavy oiling of Macondo well-sourced oil was severe along much of the Louisiana coastline. The cumulative area of oiled wetland in Louisiana was 1,055 km² (Nixon et al., 2016). The hours of toil to remove as much of the oil as possible in a manner doing no further harm to the marshes amounted to many thousands of person-years. There were some immediate, obvious impacts such as dead salt marsh vegetation, marsh fauna covered with oil, and sediments initially highly contaminated with toxic petroleum compounds. Impacts, such as a lower percent cover of living marsh vegetation and decreased population levels of some marsh fauna, were obvious for at least two years and often for four to five years. The regrowth of *S. alterniflora* in areas that were moderately to lightly oiled is encouraging, but longer-term studies of some damaged marsh shorelines showed precipitous shoreline erosion at least two and a half years after oiling due to unseen damage to belowground vegetation biomass. Faunal groups have sometimes not recovered completely. Coastal habitats are considered robust up to a point as a result of adaptation to changing and highly variable environmental parameters. Some recovery may occur, albeit with a potentially new baseline. Marshes lost due to oiling and shoreline erosion will not come back.

Out of the disaster rose a robust scientific enterprise funded with the help of government agencies, private industry, and well-funded research programs. Many data are publicly available. Data that were not readily available from the Natural Resource Damage Assessment are becoming accessible. Research continues, syntheses are well underway, and many more papers will appear. It's an old adage, but the research community is making lemonade from a lemon—a disaster. The unique opportunity to study the effects of a major oil spill on coastal habitats will result in a stronger oil spill response program well into the future but, hopefully, fewer of them. ☺

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