

Review

Response of microbial communities to oil spill in the Gulf of Mexico: A review

Linda Adzigbli^{1,2}, Hernado P. Bacosa^{3,4} and Yuewen Deng^{1,2*}

¹Pearl Research Institute, Guangdong Ocean University, Zhanjiang 524025, China.

²Fishery College, Guangdong Ocean University, Zhanjiang 524025, China.

³College of Science and Environment, Mindanao State University at Naawan, Misamis Oriental 9023, Philippines.

⁴College of Fisheries and Aquatic Sciences, Western Philippines University-Puerto Princesa Campus, Palawan 5300, Philippines.

Received 14 March, 2018; Accepted June 8, 2018

Crude oil has become a part of the marine ecosystem through natural seeps and oil spills. Microbial communities have adopted various response mechanisms to adjust to oil spills that contaminate the marine environment and help restore the ecosystem to its original state. These response mechanisms ranges from change in indigenous microbial community composition, change in microbial diversity to gene diversity and modification. An instance for review was the deep-water horizon (DWH) oil spill in the Gulf of Mexico. The DWH oil spill was distinctive from other spills in terms of profundity, extent as well as its scale hence fears and enquiries about the state and outcome of the hydrocarbons at large is required. The main inquiry was about the metabolism ability of microbial communities; the ways, and to what degree the hydrocarbons can be metabolized. Various researches after the spill revealed that change in the successional patterns from the water column, shallow water and bottomless sea sediments to the coastline sediments saw the dominance of *Roseobacter* cluster within the Alphaproteobacteria on the surface, the Deltaproteobacteria closest to the wellhead, *Cycloclasticus* in shallow oil slicks, *Colwellia* and *Alteromonas* in the deep-sea hydrocarbon plume and sediment. These microbial communities help in bioremediation of oil during oil spills through their response mechanism. Factors such as nutrient limitation, hydrocarbon availability, ocean mixing and circulation among others also limit the rate at which microbial communities degrade hydrocarbons. This review outlines the response mechanism of microorganisms and how they help in hydrocarbon degradation.

Key words: Oil spills, microbial communities, microbial response, microbial degradation, hydrocarbons, deepwater horizon, Gulf of Mexico.

INTRODUCTION

Crude oil has become a vital part of the world's economy and industrial growth and is currently in a period of industrial development, alteration and increase (Bao et al., 2014). An increase in this industry involved in

*Corresponding author. E-mail: dengyw@gdou.edu.cn.

Author(s) agree that this article remain permanently open access under the terms of the [Creative Commons Attribution License 4.0 International License](https://creativecommons.org/licenses/by/4.0/)

production, transportation and storage of oil has exposed most shores along oil mining areas and marine environment to oil spill accident (McGenity et al., 2012) from cargo/wholesale ocean carriers which are the major source carriers of oil (Bao et al., 2014). These oil spills affect human life, the environment and ecosystem as a whole. For example, the 2002 Prestige oil spill affected shores of Spain with about 66% of species abundance lost (Huz et al., 2005); the Deepwater Horizon spill (2010) conceded biodiversity of vertebrates and metazoan meiofauna (Baguley et al., 2015). Some other intense oil spill examples are the tanker collision in the Mumbai coast and the oil spill in Montora (Sakthipriya et al., 2015)

Microbial communities are known to control most major processes that occur in the marine environment (Karl, 2007). One important function and process is biodegradation of contaminants and nutrient recycling that helps to ensure an effective and efficient ecosystem (Wu et al., 2014). Hydrocarbon degradation by microorganisms has received much consideration because of its un-hazardous, inflammability, extensive and environmentally friendly state when likened to other orthodox methods (Sakthipriya et al., 2015). Microorganism from all the three domains of life are known to utilize the ~600 000 tons of oil which moves into the marine ecosystem from natural leaks yearly (NRC, 2003). A total of 175 prokaryotic genera of microorganisms from seven phyla of Bacteria, Archaea, and an equivalent amount of fungal genera, can utilize hydrocarbons as the only or main source of carbon (Hazen et al., 2015). Most of these microorganisms are found in the water column, sea bed sediments and on the shorelines of the marine environment through the tropics to the Polar Regions eg. Alphaproteobacteria, Gammaproteobacteria, Deltaproteobacteria, Pelagibacter, Actinobacteria, Planctomycetes and Bacteroidetes (Yang et al., 2016).

Upon the introduction of crude oil in the oceanic ecosystem, there is a change in microbial community consisting of numerous mutually surviving species which is described via resource sharing (Yakimov et al., 2005). The native oil utilizing bacteria becomes enriched, with organisms of the order *Oceanospirillales* comprising up to 90% of bacterial community, when related with 5% of the pure sample (Hazen et al., 2015). McNutt et al. (2012) after the DWH oil spill in the Gulf of Mexico projected ~5.0 M drums to ~210 M tons of oil and gas released. Other research from these oil spill in April 2010 discovered impacts of the oil on marine organisms populations involving corals (Goodbody-Gringley et al., 2013), meio-, macro- and mega-fauna (Fisher et al., 2014) coupled with its influence on microorganisms assemblies (Hazen et al., 2010; Edwards et al., 2011; Mason et al., 2012; Redmond and Valentine, 2012; Gutierrez et al., 2013).

This study reviews the responses of microbial communities from the introduction of oil from oil spills to the marine environment, from the water column, shallow water, and bottomless sea sediments to the coastline

sediments, in particular, with reference to the Deepwater Horizon oil spill.

CONSTITUENTS OF CRUDE OIL AND BIODEGRADATION

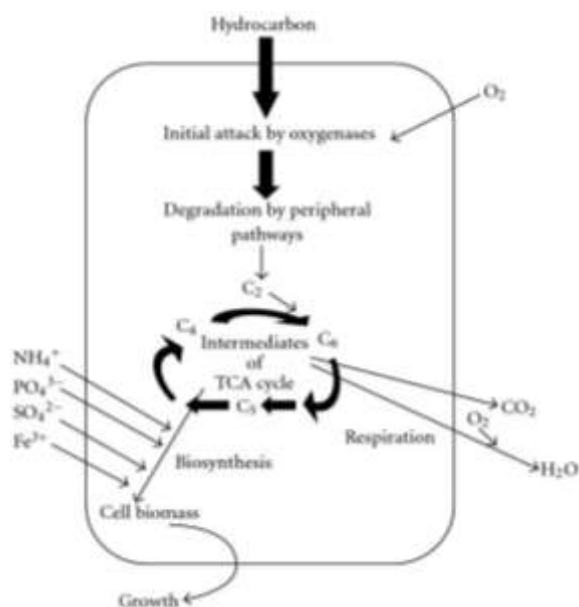
Crude oil is a composite combination of organic compounds principally consisting of hydrocarbons (HC), averagely ~30% linear and branched alkanes, ~30% cyclic alkanes, ~30% aromatics and ~10% molecules with heteroatoms such as sulphur, oxygen and nitrogen (Tissot and Welte, 1984) with the latter giving oils most of their color. The aromatics consist of molecules that contain at least one single or condensed rings and aromatic ring, coupled by recurring and linear alkane substituents like the monocyclic (Tissot and Welte, 1984). The aromatics also comprise of polycyclic aromatic hydrocarbons (PAHs). Low molecular weight compounds (benzene, naphthalene and anthracene) are favorably degraded and high molecular weight (pyrene and fluoranthenes) being also broken down (Bacosa and Inoue, 2015). The polar fractions of crude oil comprise mainly of Asphaltenes and resins; however, the characterization of this polar molecule has not yet been widely done in the marine ecosystem. Microbes are able to take up some, and others if constantly exposed to the sun are generated by photochemistry (Aeppli et al., 2012), making their gross fate in the environment unclear. Hydrocarbons with about 40 carbon atoms are near total biodegradability in a one or two months when presented with a conducive atmosphere, except for certain hopanes and steranes (Prince et al., 2013); however bigger molecules degrade much more slowly, example are the constituents intended for roads.

The introduction of oil into a marine ecosystem makes considerable excess of carbon available in the development of microorganisms (Prince et al., 2003). However, unavailability of nutrients (nitrogen and phosphorus) is able to lessen the development of microbes and hence oil degradation (Liu et al., 2017). In an attempt to promote oil degradation on diverse coastlines (including the Arctic), fertilizers containing available nitrogen and phosphorus were added (Prince et al., 2003). Wide research and field-testing discovered that the development of hydrocarbon degrading microorganisms was stimulated by adding nutrients and consequently raises the detected speed of oil decomposition (Atlas and Bragg, 2009).

Microbial degradation eliminates the hydrocarbons in marine environs and regenerates the oil polluted biota (Al-Hadhrami, 1995). Significant progress has been made within previous era in understanding hydrocarbons degradation by microorganisms (Atlas et al., 2011). The major microbes that help in degradation of oil have been identified from the 3 domains of life: bacteria, archaea and eukaryotes (Bacosa et al., 2015a) via different degradation pathways (Table 1). Most of the active oil degrading

Table 1. The major oil degrading microbes and the hydrocarbons degraded.

Taxa	Phyla	Degradation pathway/metabolism	HC degraded
Bacteria	Proteobacteria (Alpha, Beta, Gamma and Delta)	Anaerobic, aerobic/sulfate and nitrate reducer	Aromatic HC, alkylphiliic and halophilic HC, phenanthrene, PAHs, carbazole, heterocyclic aromatics, naphthalene, BTEX, mono-aromatic HC, fluoranthene, linear chain alkanes, benzo[a]pyrene, propane, ethane, butane
Bacteria	Actinobacteria	Anaerobic	Aromatic hydrocarbons (phenanthrene), PAHs
Bacteria	Cyanobacteria	Aerobic pathway	Naphthalene, n-alkanes and isoalkanes, other aromatic HC
Bacteria	Firmicutes	Anaerobic/fermentative, sulfate reducing, saprophytes	Long chain alkanes, naphthalene, pyrene, other aromatics
Bacteria	Bacteroides	Anaerobic/fermentative, nitrogen reducing	Carbazole, PAHs, benzo[a]pyrene
Bacteria	Deinococcus-thermus	Aerobic	Hexadecane and a broad spectrum of PAHs, toluene
Archaea	Halobacteria	Aerobic/ nitrate reducers	Phenanthrene, benzene, toluene, n-Alkane, octadecane, heptadecane
Archaea	Euryarchaeota	Anaerobic/ Fermentative Methanogen,	Methane
Eukaryote	Fungi	Aerobic	Alkanes

**Figure 1.** Principle for hydrocarbon breakdown (Das and Chandran, 2011).

main and exclusive origin of energy among those with the ability to breakdown or convert hydrocarbons (Head et al., 2006). The oceanic ecosystem only shelters a minimal of 25 genera of bacteria that decompose hydrocarbons and are known primarily for pollutants attenuation (Das and Chandran, 2011). Due to the diversified nature of hydrocarbon compounds related to oil (iso-, cyclo, and linear alkanes, monoaromatic compounds and polycyclic aromatic hydrocarbons), the breakdown of different groups of hydrocarbon compounds needs different microorganisms with distinct biochemical mechanisms (Timmis et al., 2010). Distinctively, microbial communities have the ability to biologically breakdown a large array of hydrocarbons collectively as compared to an individual microorganism. Succeeding the DWH spill, there was a fast improvement in the quantity of hydrocarbon-degrading microorganisms in the water column, shallow and subsurface column water and ruled by recognized hydrocarbon-decomposing bacteria (King et al., 2015).

The degradation of hydrocarbons by microorganisms mostly involves oxygen combined with hydrocarbons to produce water and carbon dioxide achieved by the enzymes oxygenase and peroxidase (Figure 1). Hence, free oxygen is required for degradation to occur through these pathways. Shallow waters hardly lack oxygen; however, the concentration of oxygen can reduce as it travels through the water column and sometimes lacking

microbes are bacteria and over 79 genera of bacteria have been known to be able to use hydrocarbons as the

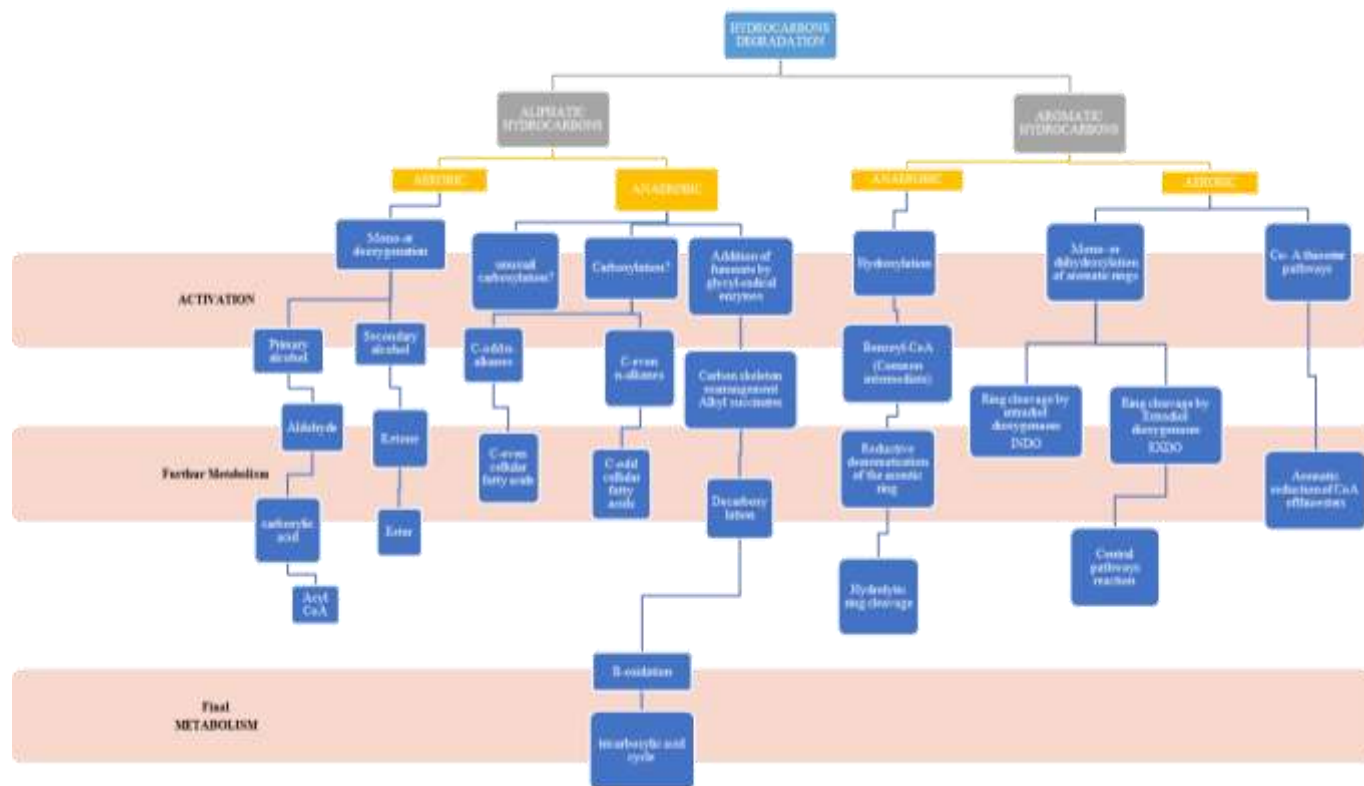


Figure 2. Pathway for microbial degradation of hydrocarbon.

Table 2. The enzymes involved in specific hydrocarbon degradation (Nilanjana and Preethy, 2011).

Enzymes	Substrates
Soluble-methane monooxygenases	C1–C8 alkanes alkenes and cycloalkanes
Particulate-methane monooxygenases	C1–C5 (halogenated) alkanes and cycloalkanes
AlkB-related, hydroxylases, alkane	C5–C16 alkanes, fatty acids, alkyl benzenes, cycloalkanes and so forth
Eukaryotic P450	C10–C16 alkanes, fatty acids
Bacterial P450 oxygenase system	C5–C16 alkanes, cycloalkanes
Dioxygenases	C10–C30 alkanes

in bottom waters. Most often, sediments usually lack oxygen (anoxic condition) below the surface; however, in some cases, oxygen is able to infiltrate below to the seabed (Roy et al., 2012). It is unlikely for anoxic condition on shallow slicks of the water plume to prevent or reduce biodegradation due to the ability of oil droplets to dilute quickly. Anoxic conditions can however occur in lower levels or bottom depths depending on the oil concentration and degree of oxygen renewal by waves and currents. The degradation of hydrocarbons by microorganisms via aerobic pathways (Figure 2) is known as aerobic biodegradation of hydrocarbons. The Gammaproteobacteria, Alphaproteobacteria and Betaproteobacteria are the major oil-degrading bacteria that utilize oxygen and are mostly outlined (Head et al.,

2006; Van Beilen and Funhoff, 2007).

Biodegradation by aerobic microorganisms is activated by monooxygenase and dioxygenase enzymes (Austin and Callaghan, 2013). *Alcanivorax borkumensis* an oil-degrading microorganism and a marine gammaproteobacterium is widely studied and defined to consume wide array of aliphatic hydrocarbons (Dos Santos et al., 2010) through various pathways using terminal oxidation process through numerous enzymes (Table 2) introducing hydroxyl groups to the organic compounds (alkB1, P450 and cytochrome monooxygenase) (Sabirova et al., 2006).

Despite the fact that hydrocarbon degradation by aerobes symbolizes a fast and acknowledged method (Fritsche and Hofrichter, 2008), much consideration is

given to degradation by anaerobes (Heider and Schühle, 2013) for its role in marine ecosystems associated with oil spills (Head et al., 2006).

The scale of anaerobic hydrocarbon degradation is slow as compared to aerobic hydrocarbon degradation; however, it is mostly needed in marine sediments (Roy et al., 2012). When oxygen is limiting, Fe^{3+} , SO_4^{2-} and NO_3^- are known to occur for biodegradation of hydrocarbon (Foght, 2008). Marine harbor sediments are known to degrade petroleum hydrocarbons when oxygen is limiting and sulfate and iron-reducing conditions are present (Coates et al., 1996). For example, the Caspian Sea permanently lacks oxygen in bottom waters, so it is possible that any hydrocarbon degradation is under oxygen limitation. Microorganisms adapted to oxygen limiting conditions comprises of sulfate reducers, denitrifying and nitrate ammonifying bacteria, phototrophs, and metal ion reducers, with the ability of breaking down several hydrocarbons, ranging from n-alkanes and n-alkenes to the more stubborn aromatic compounds (Heider and Schühle, 2013).

The often discussed method for initiating and breakdown of hydrocarbon under anaerobic conditions is the addition of fumarate (Heider and Schühle, 2013). Other substitute methods defined include intra-aerobic hydroxylation, oxygen-independent hydroxylation and carboxylation (Callaghan, 2013a; Heider and Schühle, 2013) (Figure 2).

Activation for further metabolism in aerobic pathway requires terminal and sub-terminal reaction for aliphatic HCs and peripheral hydroxylation reactions for aromatic HCs. Anaerobic pathways require double reaction for this process (Garcia and Oliveira, 2013).

POST SPILL MICROBIAL RESPONSE MECHANISMS

Research over time has proven that after an oil spill incident, microbial communities mostly make use of 3 major response mechanism from the water column, surface water and bottomless sea sediments to the shoreline sediments mainly change in succession of native microbial community structure, change in microbial diversity and gene diversity and modification (Engel and Gupta, 2014; Rodriguez et al., 2015).

For instance, with respect to DWH oil spill, discharge was a Louisiana lighter crude oil (contains little sulfur and great gasoline/kerosene fractions as compared to denser oils); dominated by alkanes (saturated hydrocarbons), 16% aromatic hydrocarbons and 10% polar compounds (Reddy et al., 2012). Shortly succeeding the blast, shallow waters were covered with huge quantities of oil. However assumptions were undiscovered but then possibly bulky quantities of oil was confined in deep waters due to the great depth. In the first month of the DWH accident, a bottomless water oil column interrelated with dispersed MC252 oil was discovered at ~1100 m depth (Hazen et

al., 2010). The column was composed of a composite combination of hydrocarbons comprising of alkanes, monoaromatic hydrocarbons (BTEX) and polycyclic aromatic hydrocarbons (PAHs) with concentrations up to 189 $\mu\text{g/L}$ (ppb) and extending principally in a west-south west direction from the still gushing wellhead (Reddy et al., 2012). These hydrocarbons are more often than not differentiated by known biomarkers and their corresponding fractions. Additionally, constituents of natural gas; methane, ethane and propane too was discovered at significant, then again doubtful levels (Joye et al., 2011; Reddy et al., 2012). This composite combination of hydrocarbons discharged at bottomless waters and in cold waters (4 to 6°C) lead to microbial biomass bloom in the column (Hazen et al., 2010).

In the water column, it was noticed that there was a substantial difference and variety deficit in deep and shallow oil slick populations when compared with populations at the non-oil impacted water column. This was due to the phylogenetic shift undergone by the indigenous populations (Redmond and Valentine, 2012; Yang et al., 2016). Findings according to Liu et al. (2017) stated the role of environmental factors especially temperature on microbial succession and shift. Further discoveries stated that succession patterns at every specific location were determined by the availability of specific hydrocarbon compounds (Dubinsky et al., 2013). The carbon branded hydrocarbons and segregation methods gave extra proof of fluctuating populations of impacted water column with ability of disintegrating several groups of hydrocarbons (Gutierrez et al., 2013). The 16S rRNA studies of microorganisms sample within the first and second month after the DWH spill saw the dominance of an uncultivated gammaproteobacterium from order *Oceanospirillales* dominating (Hazen et al., 2010; Redmond and Valentine, 2012; Mason et al., 2012). Even though GeoChip 4.0 submitted proof of enriched genes included in aerobic and anaerobic hydrocarbon degradation in the column, metatranscriptomic data obtained from the same cruise samples suggested aerobic degradation of hydrocarbons as most dominant on site procedure during that time (Mason et al., 2012). Genes that help in aerobic alkane degradation (e.g., alkane monooxygenase, cyclohexanol dehydrogenase and cyclohexanone monooxygenase) remained highly at significant peaks in the column metatranscriptomes. These genes were also found in single-cell genomes of *Oceanospirillales*, however aromatic hydrocarbon degradation were discovered in low levels or remained undiscovered (Mason et al., 2012). Around mid- to late June 2010, there was change in succession of microbial community in the water column, dominantly by two different gammaproteobacteria groups, *Cycloclasticus* and *Colwellia* (Redmond and Valentine, 2012). With regards to microcosm experiments, the crude oil enriched areas (methane, ethane, propane and benzene) were dominated by *Colwellia* spp., hence the anticipation of its

essential role of degrading ethane and propane *in situ* within this period (Redmond and Valentine, 2012). Transcriptomic data further revealed that the *Colwellia* spp. was active and succeeded preceding Oceanospirillales because of their gaseous and aromatic hydrocarbon degradation ability (Mason et al., 2014a). The *Colwellia* spp. experienced a bloom in June 2010 even though they were scarce in the column during late May 2010 (Mason et al., 2012). By September 2010, initially discovered microorganisms (*Oceanospirillales Cycloclasticus* and *Colwellia*) were substituted by initially undiscovered methylotrophic bacteria (*Methylococcaceae*, *Methylophaga* and *Methylophilaceae*), *Flavobacteria* and *Rhodobacterales* due to the presence of methane and methane oxidation observed in minute quantities in the September plume, in addition to the enrichments achieved by the September plume samples (Redmond and Valentine, 2012). Later in October 2010 and July 2011, the analysis of microbial community composition (clone libraries and pyrosequencing) from post-column samples showed likeness for the pre-spill pelagic community (800 m, March 2010) (Yang et al., 2016).

The surface water of the Gulf of Mexico in May 2010 showed dominating population of gammaproteobacteria and *cycloclasticus* (known to degrade aromatic hydrocarbons), similar to that of the deep water plume (Yang et al., 2016). However, pyrosequencing of oil mounds and clone library studies from other distinct sites within this same period showed a dominance (above 65%) of alpha and gammaproteobacteria and cyanobacteria (Redmond and Valentine, 2012), hence highlighting the distinction of surface slick communities from the bottomless water column. There is a possibility for both shallow slick and bottomless water column undergoing the same succession changes of microbial community composition dependent on type and availability of hydrocarbons at each definite time and location.

The deep-sea sediments are a home of various microbial communities (Bacosa et al., 2018, 2015b) similar in genera with the water column. After the DWH spill, large quantity of PAH compounds (>24,000 µg/kg) were observed in deep-sea sediments near the oil platform as compared to distant cores (~50 µg/kg); hence, the uncovering of the indigenous microflora to aromatic hydrocarbons near the oil platform (OSAT-I, 2010). Metagenomic analysis and targeted functional gene assays of subsurface (1.5 to 3 cm) deep sea sediment cores from September to October 2010 was highly dominated by Deltaproteobacteria and anaerobic degrading genes for aliphatic and aromatic hydrocarbons (For example, *bssA*, benzoyl-CoA reductase genes and *assA*) in the sediments located near the well (1-3 km) in respect to the distant (128 km) control samples (Kimes et al., 2013). Alphaproteobacteria was second-most abundant and was in line with alphaproteobacterial

blooms observed in metagenomic analyses of seafloor sediments collected in September 2010 (Mason et al., 2014). Other discovered groups according to Yang et al. (2016) are the Deltaproteobacteria, Bacteroidetes, Actinobacteria, Planctomycetes and Verrucomicrobia. The abundance of the groups increased or decreased over time depending on specific hydrocarbon availability and successional changes of microbial communities observed at the order, family or genus level of the various groups (Figure 3). The presence of Oceanospirillales, even though in low quantities with no variation at contaminated and non-contaminated sites, presented the genomic proof of aerobic hydrocarbon-degradation in sediments (Kimes et al., 2013).

Metagenomic analysis of samples taken 3 years after the spill (June 2013) still revealed genes related to the initial oxidation of aromatic rings, alkane monooxygenase and those involved in metabolizing hydrocarbon degradation by-products (alcohol and cyclohexanol dehydrogenases), and fatty acid metabolism was the most abundant (Bacosa et al. In Press). Bacterial communities of *Alteromonadales*, *Oceanospirillales*, *Methylococcales*, *Rhodobacterales* and *Bdellovibrionales* increased in oil treatments.

In coastal sediments/sands, oils discovered after an oil spill were extensively weathered; mostly reducing C9-C16 n-alkanes (0.3 to 1.6% of total composition as compared to 54% in MC252 oil) and BTEX/C3-benzenes (an order of magnitude lower levels) (Liu et al., 2012). The concentrations of PAH are also altered losing the dominant MC252 PAH and naphthalene, reduced to 3-9% of total PAHs in relation to 64% in unaltered MC252 oil. However, according to Engel and Gupta (2014), coastal sandy beach had shifting regime of microbial communities with respect to depth, location and time. Some of the dominant groups found on the open beach and swash zones were Gammaproteobacteria, Alphaproteobacteria, Firmicutes, Bacteroidetes, Enterobacteriales, Xanthomonadales and Chromatiales. Successional changes occurred in the various species of these groups over time. Aeppli et al. (2012) discovered high levels (10 times less in MC252) of oxyhydrocarbons (major component of tar balls) in beach sand after a long term study (18 months after spill). Kiruri et al. (2013) discovered obstinate free radicals on coastal beach Tar balls providing evidence of the oxidation of aromatic hydrocarbons with transition metals and weathering of hydrocarbon through multiple processes. However, it should be noted that these processes vary based on the site deposited.

FACTORS AFFECTING MICROBIAL BIODEGRADATION

Microbial degradation of oil spills is a composite procedure influenced by several features of the oil and the surroundings. For example, the scope of oil droplets

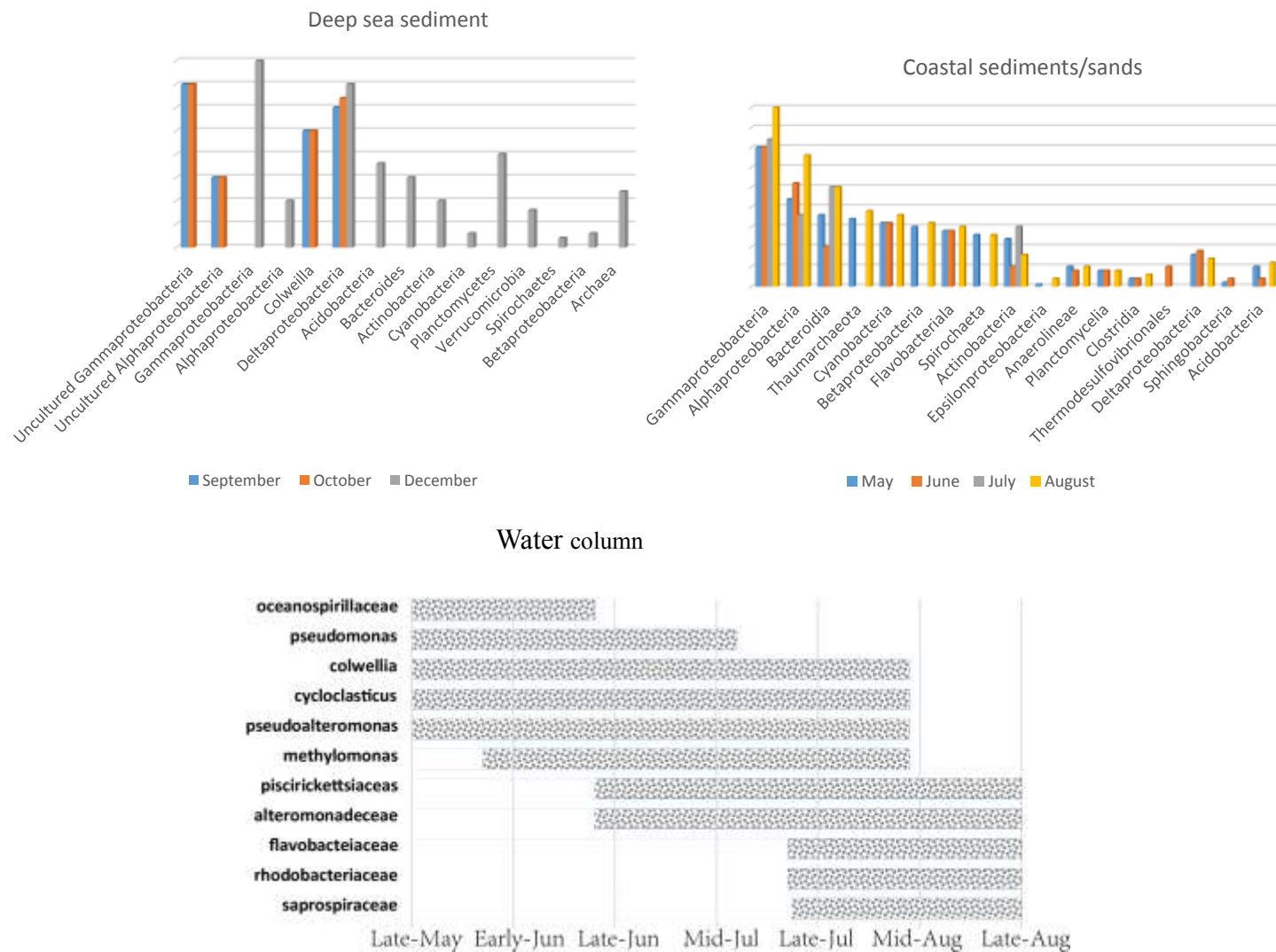


Figure 3. Overview of the relative abundance and successional change of microbial community at various sites in response to oil spills (Mason et al., 2014; Kimes et al., 2014; Rodriguez-R et al., 2015).

dissemination determines the prospects of the oil in the subsequent time frame (Yapa et al., 2012). Physical and microbial processes degrade tiny oil droplets easily (Hazen et al., 2015).

Dubinsky et al. (2013) established that the simultaneous operation of multiple hydrocarbon-degrading bacteria throughout the spill was regulated by change of hydrocarbon availability. For example, *Oceanospirillales* and *Pseudomonas* were the major genera in the initial stages of the oil spill with very high n-alkanes and cycloalkanes levels. Kleindienst et al. (2015) observed a change in deep plume community with respect to a change in quantity of hydrocarbon available (increased aromatic hydrocarbons and decreased petroleum hydrocarbons), that is, *Colwellia*, *Cycloclasticus* and *Pseudoalteromonas* dominating.

The process of biodegradation also involves degrading

transformational byproducts and exopolymeric substances yielded by microbial communities to combine hydrocarbons and enable oil availability. The measurement of a higher peptidase activity and enzymatic hydrolysis of carbohydrates in the water samples within the oil spill plume when likened to the outside predicted that, the deep-water column microbial communities were structured to degrade singled out array of explicit high molecular weight substrates (Ziervogel and Arnosti, 2014). Gutierrez et al. (2013) researched on the function of amphiphilic exopolysaccharides produced by indigenous *Halomonas* bacteria for the period of the DWH oil spill. They discovered that strain TG39 produced *Halomonas* exopolysaccharides which efficiently amplified the solubility of aromatic hydrocarbons and improved their degradation, hence influencing oil removal and oil aggregates formation.

Nutrient deficiency is a normal limiting factor for microbial growth. Nitrogen and phosphorous are known as the key restrictive elements for oil degradation in the sea (Beyer et al., 2016). In oil-contaminated shallow waters of the Northern Gulf of Mexico (NGOM), it has been proposed that deficiency of dissolved nutrients mainly phosphate, reduces microbial growth (Liu et al., 2017). This is because when incubation mixtures were altered with nutrients, bacterial cell numbers and biomass improved speedily (Edwards et al., 2011). The addition of nitrogen fertilizers mainly on shorelines and uric acid at sea help stimulate and enhance oil bioremediation (Ron and Rosenberg, 2014).

Oceanic mixing and circulation processes are essential for microbial oil degradation (Beyer et al., 2016). The assessment of the impact of physical mixing processes on marine bacterial communities showcased biodegradation patterns of a faster growth rate for bacteria from seed populations that are scarce in nature. There is possibility of major participation of oceanic mixing process in allocating hydrocarbons, accompanied by bacterial blooms, and accelerated hydrocarbon degradation across an autoinoculation effect inside the northeast Gulf waters. The impacts of mixing and circulation processes on degradation of oil spills was shown by the higher abundance of HC-degrading bacteria in past bloomed waters that later re-circulated to the spill site, feeding successive bacterial blooms (Valentine et al., 2012).

CONCLUSION

In an era where crude oil production and consumption is on the rise, oil spills are inevitable in the marine environment. Even though the frequency and quantity of oil spills have reduced over the years, the marine environment still remains a reservoir for oil from natural seeps. Microbial communities have developed the ability to degrade these crude oil products. Bacteria from the phylum Proteobacteria has been known as the major crude oil degrading microbe. Other microbial groups: Firmicutes, Bacteroidetes and some archaeal groups also have the ability to breakdown hydrocarbons. They have developed mechanisms such as acquisition of oil degrading functional genes, change in biodiversity where species with the ability to degrade specific hydrocarbons dominate and change in succession patterns. How microbial communities respond to crude oil has been far researched over the years; however, the amount and quantity of hydrocarbons degraded is still lacking. Other researches have also focused on the large fractions of oil introduced into the system leaving the residues, weathered components and the biodegraded byproducts which have detrimental effects on other marine organisms. More researches should focus on the concentration and quantity of hydrocarbons degraded by specific oil degrading microbial species and using oil

residues from past spills to assess the impacts and possible ways for total ecosystem recovery.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

REFERENCES

- Aeppli C, Carmichael CA, Nelson RK, Lemkau KL, Graham WM, Redmond MC, Valentine DL, Reddy CM (2012). Oil weathering after the deepwater horizon disaster led to the formation of oxygenated residues. *Environmental Science and Technology* 46(16):8799–8807.
- Al-Hadhrami MN, Scott LHM, Fisher PJ (1995). Bacterial survival and n-alkane degradation within Omani crude oil and a mousse. *Marine Pollution Bulletin* 30:403-408.
- Atlas R, Bragg J (2009). Bioremediation of marine oil spills: when and when not - the Exxon Valdez experience. *Microbial Biotechnology* 2(2):213-221.
- Atlas RM, Grimes DJ, Hazen TC, Spain J, Suflita, JM, Reid A, Maloy S, Cerniglia CE, King GM, Kinner NE, Kostka JE, Lee K, Loeffler F, Prince RC, Sobocky P, Steffan RJ, Teske AP, Mooy BV, Venosa AD, Wackett LP, Ward CH, Young L, Zylstra GJ (2011). Microbes and oil spills in FAQ. *American Academy of Microbiology* (Washington, DC), 1:13.
- Austin RN, Callaghan AV (2013). Microbial enzymes that oxidize hydrocarbons. *Frontiers in Microbiology* 4(10):338.
- Bao M, Pi Y, Wang L, Sun P, Lia Y, Cao L (2014). Lipopeptide bio surfactant production bacteria *Acinetobacter* sp. D3-2 and its biodegradation of crude oil. *Environmental Science: Processes and Impacts*, pp. 1-7.
- Bacosa HP, Erdner DL, Liu Z (2015a). Dierentiating the roles of photooxidation and biodegradation in the weathering of Light Louisiana Sweet crude oil in surface water from the Deepwater Horizon site. *Marine Pollution Bulletin* 95:265-272.
- Bacosa HP, Liu Z, Erdner DL (2015b). Natural sunlight shapes crude oil-degrading bacterial communities in northern Gulf of Mexico surface waters. *Frontiers in Microbiology* 6:1325
- Bacosa H, Erdner DL, Rosenheim B, Shetty P, Seitz K, Baker B, Liu Z. Hydrocarbon degradation and response of seafloor sediment bacterial community in the northern Gulf of Mexico to light Louisiana sweet crude oil. *The ISME Journal* (accepted).
- Bacosa HP, Inoue C (2015). Polycyclic aromatic hydrocarbons (PAHs) biodegradation potential and diversity of microbial consortia enriched from tsunami sediments in Miyagi, Japan. *Journal of Hazardous Materials* 283:689-697.
- Bacosa HP, Evans MM, Wang Q, Liu ZF (2018). Assessing the role of environmental conditions on the degradation of oil following the deepwater horizon oil spill. *Oil Spill Environmental Forensics Case Studies* 617-637.
- Bacosa HP, Inoue C (2015). Polycyclic aromatic hydrocarbons (PAHs) biodegradation potential and diversity of microbial consortia enriched from tsunami sediments in Miyagi, Japan. *Journal of Hazardous Materials* 283:689-697.
- Baguley JG, Montagna PA, Cooksey C, Hyland JL, Bang HW, Morrison C, Kamikawa A, Bennetts P, Saiyo G, Parsons E, Herdener M (2015). Community response of deep-sea soft-sediment metazoan meiofauna to the deepwater horizon blowout and oil spill. *Marine Ecology Progress Series* 528:127–140.
- Coates JD, Anderson RT, Woodward JC, Phillips EJP, Lovley DR (1996). Anaerobic hydrocarbon degradation in petroleum contaminated harbor sediments under sulfate-reducing and artificially imposed iron-reducing conditions. *Environmental Science and Technology* 30(9):2784-2789.
- Das N, Chandran P (2011). Microbial degradation of petroleum hydrocarbon contaminants: An overview. *Biotechnology Research International* 2011: 941810
- Dos Santos, VM Sabirova, J Timmis, KN Yakimov, MM, Golyshin PN (2010). "*Alcanivorax borkumensis*," in *Handbook of Hydrocarbon and*

- Lipid Microbiology, eds. KN Timmis, T McGenity, JR van der Meer, V de Lorenzo (Berlin; Heidelberg: Springer-Verlag), pp. 1265-1288.
- Dubansky B, Whitehead A, Miller JT, Rice CD, Galvez F (2013). Multitissue molecular, genomic, and developmental effects of the deepwater horizon oil spill on resident gulf killifish (*Fundulus grandis*). *Environmental Science and Technology* 47:5074-5082.
- Edwards BR, Reddy CM, Camilli R, Carmichael CA, Longnecker K, Van Mooy BAS (2011). Rapid microbial respiration of oil from the deepwater horizon spill in offshore surface waters of the Gulf of Mexico. *Environmental Research Letters* 6(3):9.
- Engel AS, Gupta AA (2014). Regime shift in Sandy beach microbial communities following deepwater horizon oil spill remediation efforts. *PLoS One* 9(7):e102934.
- Fisher CR, Demopoulos AWJ, Cordes EE, Baums IB, White HK, Bourque JR (2014). Coral communities as indicators of ecosystem-level impacts of the deepwater horizon spill. *BioScience* 64(9):796-807.
- Foght J (2008). Anaerobic biodegradation of aromatic hydrocarbons: pathways and prospects. *Journal of Molecular Microbiology and Biotechnology* 15(2-3):93-120.
- Fritsche W, Hofrichter M (2008). Aerobic degradation by microorganisms, in *Biotechnology: Environmental Processes II*, 2nd Edn. Vol. 11b, eds H.-J. Rehm and G. Reed (Weinheim, Germany: Wiley-VCH Verlag GmbH), pp. 144-164.
- Garcia INS, Oliveira VMD (2013). Microbial hydrocarbon degradation: efforts to understand biodegradation in petroleum reservoirs. *Biodegradation- Engineering and Technology*, pp. 227-236.
- Goodbody-Gringley G, Wetzel DL, Gillon D, Pulster E, Miller A, Ritchie KB (2013). Toxicity of deepwater horizon source oil and the chemical dispersant, Corexits 9500, to coral larvae. *PLoS One* 8(1):e45574.
- Gutierrez T, Berry D, Yang TT, Mishamandani S, McKay L, Teske A, Aitken M (2013). Role of bacterial Exopolysaccharides (EPS) in the fate of the oil released during the deepwater horizon oil spill. *PLoS One* 8(6):e67717.
- Hayes MHB (2006). Solvent systems for the isolation of organic components from soils. *Soil Science Society of America Journal* 70(3):986-994.
- Hazen TC, Dubinsky EA, DeSantis TZ, Andersen GL, Piceno YM, Singh N, Jansson JK, Probst A, Borglin SE, Fortney JL, Stringfellow WT, Bill M, Conrad ME, Tom LM, Chavarria KL, Alusi TR, Lamendella R, Joyner DC, Spier C, Baelum J, Auer M, Zemla ML, Chakraborty R, Sonnenthal EL, D'haeseleer P, Holman HY, Osman S, Lu Z, Van Nostrand JD, Deng Y, Zhou J, Mason OU (2010). Deep-sea oil plume enriches indigenous oil-degrading bacteria. *Science* 330:204-208.
- Hazen T C, Prince R C, Mahmoudi N (2015). Marine oil biodegradation. *Environmental Science and Technology* 50(5):2121.
- Head IM, Jones DM, Röling WFM (2006). Marine microorganisms make a meal of oil. *Nature Reviews Microbiology* 4:173-182.
- Head IM, Gray ND, Larter SR (2014). Life in the slow lane; biogeochemistry of biodegraded petroleum containing reservoirs and implications for energy recovery and carbon management. *Frontiers in Microbiology* 5(566):566.
- Heider J, Schühle K (2013). Anaerobic biodegradation of hydrocarbons including methane, in *The Prokaryotes-Prokaryotic Physiology and Biochemistry*, eds. E. Rosenberg, E. DeLong, S. Lory, E. Stackebrandt, and F. Thompson (Berlin; Heidelberg: Springer-Verlag) pp. 605-634.
- Huz RDL, Lastra M, Junoy J, Castellanos C, Vieitez JM (2005). Biological impacts of oil pollution and cleaning in the intertidal zone of exposed sandy beaches: preliminary study of the "Prestige" oil spill. *Estuarine, Coastal and Shelf Science* 65(1):19-29.
- Jonny B, Hilde CT, Torgeir B, Peter VH, Tracy KC (2016). Environmental effects of the deepwater horizon oil spill: a review. *Marine Pollution Bulletin* 10:28-51.
- Joye SB, Leifer I, MacDonald IR, Chanton JP, Meile CD, Teske AP et al (2011a). Comment on a persistent oxygen anomaly reveals the fate of spilled methane in the deep Gulf of Mexico. *Science* 332:1033.
- Joye SB, MacDonald IR, Leifer I, Asper V (2011b). Magnitude and oxidation potential of hydrocarbon gases released from the BP oil well blowout. *Nature Geoscience* 4:160-164.
- Kai Z, Arnosti C (2016). Enhanced protein and carbohydrate hydrolyses in plume associated deepwaters initially sampled during the early stages of the Deepwater Horizon oil spill. *Deep-Sea Res. II Topical Studies in Oceanography* 129:368-373.
- Karl DM (2007). Microbial oceanography: paradigms, processes and promise. *Nature Reviews Microbiology* 5(10):759-769.
- Kasai Y, Kishira H, Harayama S (2002). Bacteria belonging to the genus *Cycloclasticus* play a primary role in the degradation of aromatic hydrocarbons released in a marine environment. *Applied and Environmental Microbiology* 68:5625-5633.
- Kim SJ, Kwon KK (2010). Marine, hydrocarbon-degrading alphaproteobacteria in *Handbook of Hydrocarbon and Lipid Microbiology*, eds K. N. Timmis, T. McGenity, J. R. van der Meer and V. de Lorenzo. (Berlin; Heidelberg: Springer-Verlag) pp. 1707-1714.
- Kimes NE, Amy VC, Joseph MS, Pamela JM (2014). Microbial transformation of the deepwater horizon oil spill-past, present, and future perspectives. *Front. Microbiol.* 5 (603):603
- Kimes NE, Callaghan AV, Aktas DF, Smith WL, Sunner J, Golding B, Drozdowska M, Hazen TC, Suflija JM, Morris PJ (2013). Metagenomic analysis and metabolite profiling of deep-sea sediments from the Gulf of Mexico following the deep water horizon oil spill. *Frontiers in Microbiology* 4(50):50
- King GM, Kostka JE, Hazen TC, Sobecky PA (2015). Microbial responses to the deepwater horizon oil spill: from coastal Wetlands to the deep sea. *Annual Review of Marine Science* 7:377-401.
- Kiruri LW, Dellinger B, Lomnicki S (2013). Tar balls from Deep Water Horizon oil spill: environmentally persistent free radicals (EPFR) formation during crude weathering. *Environmental Science and Technology* 47:4220-4226.
- Kleindienst S, Grim S, Sogin M, Bracco A, Crespo-Medina M, Joye SB (2015). Diverse, rare microbial taxa responded to the deepwater horizon deep-sea hydrocarbon plume. *International Society for Microbial Ecology Journal* 1-16.
- Liu J, Bacosa HP, Liu Z (2017). Potential Environmental Factors Affecting Oil-Degrading Bacterial Populations in Deep and Surface Waters of the Northern Gulf of Mexico. *Frontiers in Microbiology* 7:2131.
- Liu Z, Liu J (2013). Evaluating bacterial community structures in oil collected from the sea surface and sediment in the northern Gulf of Mexico after the deepwater horizon oil spill. *Microbiology Open* 2:492-504.
- Liu Z, Liu J, Zhu Q, Wu W (2012). The weathering of oil after the deepwater horizon oil spill: insights from the chemical composition of the oil from the sea surface, salt marshes and sediments. *Environmental Research Letters* 7(3):035302.
- Mason OU, Hazen TC, Borglin S, Chain PS, Dubinsky EA, Fortney JL, Han J, Holman HY, Hultman J, Lamendella R, Mackelprang R, Malfatti S, Tom LM, Tringe SG, Woyke T, Zhou J, Rubin EM, Jansson JK (2012). Metagenome, metatranscriptome and single-cell sequencing reveal microbial response to Deepwater Horizon oil spill. *International Society for Microbial Ecology Journal* 6:1715-1727.
- Mason OU, Han J, Woyke T, Jansson JK (2014a). Single-cell genomics reveals features of a *Colwellia* species that was dominant during the deepwater horizon oil spill. *Frontiers in Microbiology* 5:332.
- Mason OU, Scott NM, Gonzalez A, Robbins-Pianka A, Baelum J, Kimbrel J, Bouskill NJ, Prestat E, Borglin S, Joyner DC, Fortney JL, Jurelevicius D, Stringfellow WT, Alvarez-Cohen L, Hazen TC, Knight R, Gilbert JA, Jansson JK (2014). Metagenomics reveals sediment microbial community response to Deepwater Horizon oil spill. *International Society for Microbial Ecology Journal* 8:1464-1475.
- McGenity TJ, Folwell BD, McKew BA, Sanni GO (2012). Marine crude-oil biodegradation: a central role for interspecies interactions. *Aquatic Biosystems* 8(10):10-1186
- McNutt MK, Camilli R, Crone TJ, Guthrie GD, Hsieh PA, Ryerson TB, Savas O, Shaffer F (2012). Review of flow rate estimates of the deepwater horizon oil spill. *Proceedings of the National Academy of Sciences of the United States of America* 109 (50):20260-20267.
- National Research Council (NRC) (2003). *Oil in the Sea III: Inputs, Fates, and Effects*. The National Academies Press.
- OSAT-I (2010). Summary report for sub-sea and sub-surface oil and dispersant federal on-scene coordinator, deepwater horizon MC252. Available online at: http://www.restorethegulf.gov/release/2011/07/29/osat_summary_report_sub-sea_and_sub-surface_oil_and_dispersant_detection_ecotoxic_Detection_Sampling_and_Monitoring, Paul F.

- Zukunft, RADM, US Coast Guard.
- Passow U, Ziervogel K, Asper V, Diercks A (2012). Marine snow formation in the aftermath of the deepwater horizon oil spill in the Gulf of Mexico. *Environmental Research Letters* 7(3):35301-35311.
- Prince RC, Gramain A, McGenity TJ (2010). Prokaryotic hydrocarbon degraders in *Handbook of Hydrocarbon and Lipid Microbiology*, eds K. N. Timmis, T. McGenity, J. R. van der Meer, and V. de Lorenzo (Berlin; Heidelberg: Springer-Verlag) pp. 1669-1692.
- Prince RC, Lessard RR, Clark JR (2003). Bioremediation of marine oil spills. *Oil and Gas Science and Technology* 58(4):463-468.
- Prince RC, McFarlin KM, Butler JD, Febbo EJ, Wang FCY, Nedwed TJ (2013). The primary biodegradation of dispersed crude oil in the sea. *Chemosphere* 90(2):521-526.
- Redmond MC, Valentine DL (2012). Natural gas and temperature structured a microbial community response to the deepwater horizon oil spill. *Proceedings of the National Academy of Sciences of the United States of America* 109:20292-20297.
- Reddy CM, Arey JS, Seewald JS, Sylva SP, Lemkau KL, Nelson RK, et al (2012). Composition and fate of gas and oil released to the water column during the deepwater horizon oil spill. *Proceedings of the National Academy of Sciences of the United States of America* 109:20229-20234.
- Redmond MC, Valentine David L (2012). Natural gas and temperature structured a microbial community response to the deepwater horizon oil spill. *Proceedings of the National Academy of Sciences of the United States of America* 109(50):20292-20297.
- Rodriguez LM, Overholt WA, Hagan C, Huettel M, Joel E Kostka, Konstantinos T Konstantinidis (2015). Microbial community successional patterns in beach sands impacted by the deepwater horizon oil spill. *International Society for Microbial Ecology Journal* 9:1928-1940.
- Ron EZ, Rosenberg E (2014). Enhanced bioremediation of oil spills in the sea. *Current Opinion in Biotechnology* 27:191-194.
- Roy H, Kallmeyer J, Adhikari, RR, Pockalny R, Jorgensen BB, D'Hondt S (2012). Aerobic microbial respiration in 86-million-year-old deep-sea red clay. *Science* 336(6083):922-925.
- Sakthipriya N, Doble M, Sangwai JS (2015). Bioremediation of coastal and marine pollution due to crude oil using a microorganism *Bacillus subtilis*. *Procedia Engineering* 116:213-220
- Terry C Hazen, Roger C Prince, Nagissa M (2016). Marine oil biodegradation. *Environmental Science and Technology* 50:2121-2129.
- Timmis KN, McGenity T, van der Meer JR, de Lorenzo V (2010). *Handbook of hydrocarbon and lipid microbiology*. Berlin; Heidelberg: Springer Verlag.
- Tissot BP, Welte DH (1984). *Petroleum formation and occurrence*. Petroleum formation and occurrence. Springer-Verlag.
- Valentine DL, Mezic I, Macesic S, Crnjacic-Zic N, Ivic S, Hogan PJ (2012). Fonoberov VA, Loire S. Dynamic autoinoculation and the microbial ecology of a deep water hydrocarbon irruption. *Proceedings of the National Academy of Sciences of the United States of America* 109:20286-20291.
- Valentine MM, Benfield MC (2013). Characterization of epi benthic and demersal megafauna at Mississippi Canyon 252 shortly after the deepwater horizon oil spill. *Marine Pollution Bulletin* 77(1):196-209.
- Van Beilen JB, Funhoff EG (2007). Alkane hydroxylases involved in microbial alkane degradation. *Applied Microbiology and Biotechnology* 74:13-21.
- White HK, Hsing PY, Cho W, Shank TM, Cordes EE, Quattrini AM, Nelson RK, Camilli R, Demopoulos AWJ, German CR, Brooks JM, Roberts HH, Shedd W, Reddy CM, Fisher CR (2012). Impact of the deepwater horizon oil spill on a deep-water coral community in the Gulf of Mexico. *Proceedings of the National Academy of Sciences of the United States of America* 109(50):20303-20308.
- Wu B, Lan T, Lu D, Liu Z (2014). Ecological and enzymatic responses to petroleum contamination. *Environmental Science: Processes and Impacts* 16:1501-1509.
- Yakimov MM, Denaro R, Genovese M, Cappello S, Auria GD, Chernikova TN, Timmis KN, Golyshin PN, Giuliano L (2005). Natural microbial diversity in superficial sediments of Milazzo Harbor (Sicily) and community successions during microcosm enrichment with various hydrocarbons. *Environmental Microbiology* 7:1426-1441.
- Yang T, Nigro LM, Gutierrez TD, Ambrosio L, Joye SB, Highsmith R, Teske A (2016). Pulsed blooms and persistent oil-degrading bacterial populations in the water column during and after the deepwater horizon blowout. *Deep-Sea Res. Part II*: 129:282-291.
- Yang T, Speare K, McKay L, MacGregor BJ, Joye SB, Teske A (2016). Distinct bacterial communities in surficial seafloor sediments following the 2010 deep water horizon blowout. *Frontiers in Microbiology* 7:1384.
- Yapa PD, Wimalaratne MR, Dissanayake AL, DeGraff JA (2012). How does oil and gas behave when released in deepwater? *Journal of Hydro-environment Research* 6:275-285.