Marine Oil Biodegradation

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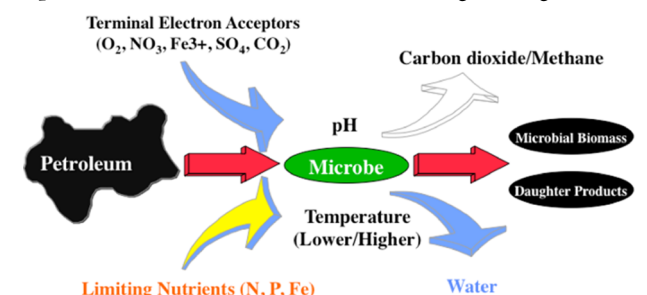
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Crude oil has been part of the marine environment for millions of years, and microbes that use its rich source of energy and carbon are found in seawater, sediments, and shorelines from the tropics to the polar regions. Catastrophic oil spills stimulate these organisms to "bloom" in a reproducible fashion, and although oil does not provide bioavailable nitrogen, phosphorus or iron, there are enough of these nutrients in the sea that when dispersed oil droplets dilute to low concentrations these low levels are adequate for microbial growth. Most of the hydrocarbons in dispersed oil are degraded in aerobic marine waters with a half-life of days to months. In contrast, oil that reaches shorelines is likely to be too concentrated, have lower levels of nutrients, and have a far longer residence time in the environment. Oil that becomes entrained in anaerobic sediments is also likely to have a long residence time, although it too will eventually be biodegraded. Thus, data that encompass everything from the ecosystem to the molecular level are needed for understanding the complicated process of petroleum biodegradation in marine environments.

1. INTRODUCTION

The world's oceans are our largest contiguous ecosystem, and microbes play a central role in the processes that occur there.[1] One that has been going on for millions of years is the biodegradation of crude oil, and microbes from all three domains of life exploit the ~600 000 tonnes of oil that annually enters the marine environment from natural seeps.[2] It is often forgotten that petroleum is a natural product formed from algae that were deposited in marine and lacustrine sediments millions of years ago, buried, and subjected to high temperatures and pressures over millions of years (Box 1). While the diagenesis and potential subsequent degradation of crude oils in reservoirs[3,4] lead to differences in the composition of different oils, all contain molecules that are clearly related to compounds found in marine algae.[5] Thus, microorganisms have been using these compounds since the beginning of biology, and it is no surprise that such organisms are found in all marine environments perfecting their ability to utilize the diverse components of crude oil, especially in the carbon-starved oceans of the world.

2. MICROORGANISMS THAT DEGRADE PETROLEUM HYDROCARBONS

Some 175 prokaryotic genera in seven phyla of Bacteria and Archaea, and a similar number of fungal genera, can use hydrocarbons as their sole or major carbon source (Figure 1). With the explosive advances in genomic technologies over the last 10 years, allowing us to identify and characterize microorganisms without having to grow them in pure cultures, we confidently expect our knowledge of the diversity of known oil-degraders to increase dramatically. Indeed it is a demonstration of the progress of marine microbiology that many of what we now perceive as the most important oil degrading microbes have only been identified in the last 20 years (e.g., *Cycloclasticus*,[13] *Alcanivorax*,[14] *Fundibacter*,[15] *Oleispira*[16])

2.1. Marine Bacterial Hydrocarbon Degradation.
Bacteria are able to degrade many hydrocarbons under both aerobic and anaerobic conditions,[4,17] and different locations in the marine environment are home to these distinct physiologies. Thus, aerobic hydrocarbon degrading microbes are found throughout the marine water column and in oxic sediments even in deep waters[7] whereas anaerobic hydrocarbon degraders are primarily found in anoxic sediments and within hydrocarbon seeps.[18] Oil biodegradation occurs readily at depth (2000−5000 m),[19,20] in the Arctic[21] and Antarctic,[22] and even in polar ice.[23]

Box 1. Crude Oils and Their Biodegradability

The average age of the oil in commercial reservoirs is about 100 million years[6] Crude oils are principally hydrocarbons—on average ~30% linear and branched alkanes, ~ 30% cyclic alkanes, ~ 30% aromatics (molecules that contain at least one aromatic ring, usually with cyclic and linear alkane substituents) and ~10% molecules with heteroatoms such as S, O, and N[6] the latter give oils most of their color. Gas chromatography is the technique of choice for analyzing the hydrocarbons up to those with about 40 C atoms. These molecules are biodegraded almost completely in a month or two under appropriate conditions, with the exception of some hopanes and steranes[7] but larger molecules, such as those found in materials destined for roadways, obviously degrade much more slowly. The polar molecules have not yet been extensively characterized; some are consumed by microbes,[8] but others are generated by photochemistry if oil remains exposed to the sun,[9,10] and their overall fate in the environment is not yet clear. After extensive biodegradation, the residual material, principally polars, is essentially indistinguishable from soil humins.[11]

An important indicator of value is the API (American Petroleum Institute) gravity, measured in degrees:

$$\text{APIGravity} = \frac{141.5}{\text{specificgravity}} - 131.5$$

Thus, distilled water has an API gravity of 10°. Oils with API gravities >40° are usually said to be "light" oils, while those with API gravities <17° are said to be "heavy". Note that almost all crude oils float on water at equilibrium; only those with API gravities <7 will sink in seawater unless they absorb denser material. Since hydrocarbons have low density, their preferential removal by biodegradation leads to oils become progressively denser as biodegradation proceeds, and likely contributes to the phenomenon of "dirty snow".[12]

As noted above, natural seeps likely contribute the majority of oil that enters the oceans every year, with the next largest fraction coming from delocalized runoff from human activities.[2] Nevertheless catastrophic oil spill are the most concentrated inputs, and they rightfully garner significant public attention. Fortunately they are becoming less frequent,[24] but oil spills have resulted in contamination of shorelines around the world.

Modern molecular tools are beginning to be applied to understand the microbes involved in the biodegradation that eventually removes the mess (Table 1).

Here we focus on biodegradation offshore and in the deep ocean, since these have become more relevant in light of the disposition of oil from the *Deepwater Horizon* spill in the Gulf of Mexico.[25] The deep ocean is a distinct environment from polar surface water in that, while the temperatures are cold, the environment is in darkness and under high pressures. Therefore, it is possible that distinct communities of oil degraders thrive in the deep ocean and in polar surface water. Some 400 000 to 1 000 000 barrels of oil go into the Gulf of Mexico every year through natural seeps on the seafloor[2] and this has likely been going on for millions of years. Thus, the microbial community may be "pre-adapted" to oil and respond more readily to oil than in other parts of the world. The *Deepwater Horizon* oil spill resulted in oil accumulating at the surface and in a dilute deep-water—oil plume, and the microbial communities responded in both settings. *Gammaproteobacteria* were dominant in both the surface and the deep-water, but the types were distinct. *Pseudoalteromonas*, *Pseudomonas*, *Vibrio*, *Acinetobacter*, and *Alteromonas* predominated in the warm surface waters, whereas the dominant organisms in the 4 °C deep-water were *Oceanospirillales*, *Colwellia*,, and *Cycloclasticus* (Figure 2).[26,27] In both settings the microbial communities degraded at least some hydrocarbon components of the released oil with a half-life of days when the oil was dispersed as dilute small droplets.[40] The uncontaminated areas at the same depth, and samples taken at the same sites before the DWH spill, were dominated by *Alphaproteobacteria*, *Pelagibacter*, and *Actinobacteria* (Figure 2). There were no significant differences between samples taken before the spill and an uncontaminated site near the spill at the same depth during the spill.[28]

Preliminary data from multiple deep-sea hydrocarbon basins around the world (Eastern Mediterranean sea, the Great Australian Bight, and the Caspian Sea) have confirmed many of the findings from the deep water in the Gulf of Mexico.[29−32] Oil-degrading microbes are always present, and relatives of the *Oceanospirilalles*, *Colwellia* and *Cycloclasticus* routinely bloom when deep-water from these locations is amended with oil and COREXIT 9500. These genera appear to be cosmopolitan cold-adapted oil degraders in polar surface waters and the deep ocean around the world.
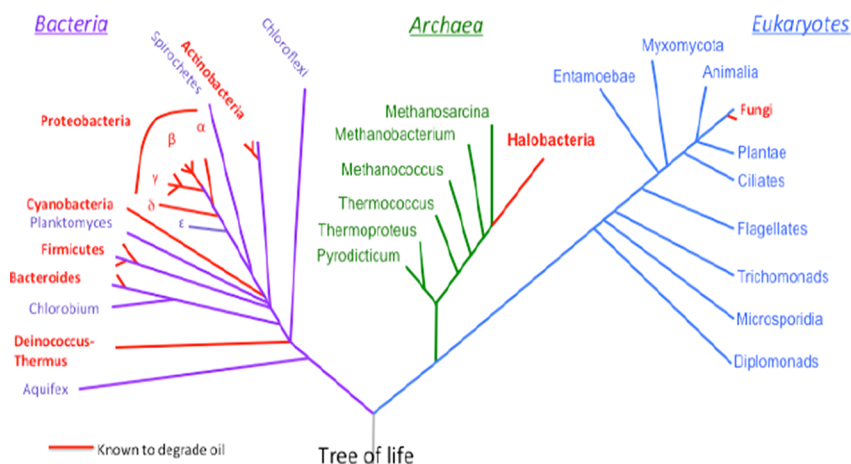

Figure 1. Oil degrading microbial taxa. Oil degrading microbial phyla, highlighted in red, have been identified from all three domains of life.[17]

Table 1. Examples of Work Using Modern Molecular Probes to Investigate Microbial Processes Following Exposure to Spilled Oil

location	exposure	microbial response
Arctic	Experimental heavy fuel oil spill, shoreline, Svalbard	*Proteobacteria* enriched.[59]
Arctic	Svalbard Sea ice exposed to oil	*Colwellia* sequences were the most abundant in oil-polluted ice and were not detected in clean ice.[23]
Arctic	Oil biodegradation at −1 °C in water from Chukchi sea	46−61% of the oil hydrocarbon was degraded over the course of the 60-day experiment.[60]
Sea of Japan	1997 Nakhodka spill. 6200 tonnes of medium fuel oil spilled in the Sea of Japan—another 10 000 tonnes thought to be slowly releasing from the sunken vessel	*Bacteroidetes, Alphaproteobacteria* and *Cyanobacteria* dominated oil-impacted seawater. A fertilized microcosm was dominated by *Alcanivorax* within the first week.[61,62]
Atlantic	Microcosms from a sandy shore. Weathered Forties crude oil added to sand microcosms; nutrients added to some. Artificial seawater used—oil added as emulsion at 3.7 kg/m², and	*Gammaproteobacteria* (especially *Alcanivorax.* and *Fundibacter*) dominated all microcosms 6 days into the experiment. Twenty days later, *Gammaproteobacteria* remained dominant in the oil-only treatment, whereas *Alphaproteobacteria* (especially *Erythrobacter*) dominated the nutrient-amended microcosm.[63]
Atlantic	Water from Trondheim fjord incubated with oil at 0 and 5 °C.	The majority of sequences recovered were *Gammaproteobacteria* and *Bacteriodetes.* Several highly similar to *Psychromonas arctica* and *Oleispira antarctica.* Archaea decreased during incubation.[44]
Atlantic	Transect from the Caribbean to South Africa with pelagic bacteria enriched by culture, and then characterized for alkane degradation genes	177 bacterial isolates representing 43 genera were obtained from 18 oil-degrading consortia.[64]
Atlantic	Microcosms in Bangor (Menai Straits, Irish Sea), Helgoland (North Sea) and Messina (Messina Straits, Mediterranean Sea). Weathered Arabian Light crude oil added at 500 ppm, with substantial slow-release nutrients up to N:C = 1:10	Microbial communities very similar at all sites after the addition of oil, with *Alcanivorax* spp. dominant. *Cycloclasticus* and *Phaeobacter* also a significant portion of the oil-impacted microbial communities, but differences in diversity at each site.[65]
Mediterranean	Mud volcanoes - natural seeps	Flavobacteria, Methylococcales, and Thiotrichales more abundant than in nearby 'unimpacted' samples.[32]
Caspian	Microbial diversity in sediments assessed by phospholipids and culture-independent sequencing.	Surface sediments collected from bottom waters with low oxygen levels dominated by *Gammaproteobacteria* while hypoxic bottom waters were dominated by *Deltaproteobacteria*, specifically sulfate-reducing bacteria. *Thaumarchaeota* were dominant in all surface sediments suggesting that nitrogen cycling is strongly influenced by ammonia-oxidizing archaea.[30]
Gulf of Mexico	2010 Deepwater Horizon Oil impacted shorelines	Contaminated samples had higher abundance of alpha and gammaproteobacteria. Successional changes were noted.[66−68]
Gulf of Mexico	Uncontaminated deepwater exposed to oil + dispersant	An increase in abundance of Colwellia and Oceanospirillales during the incubations.[69]
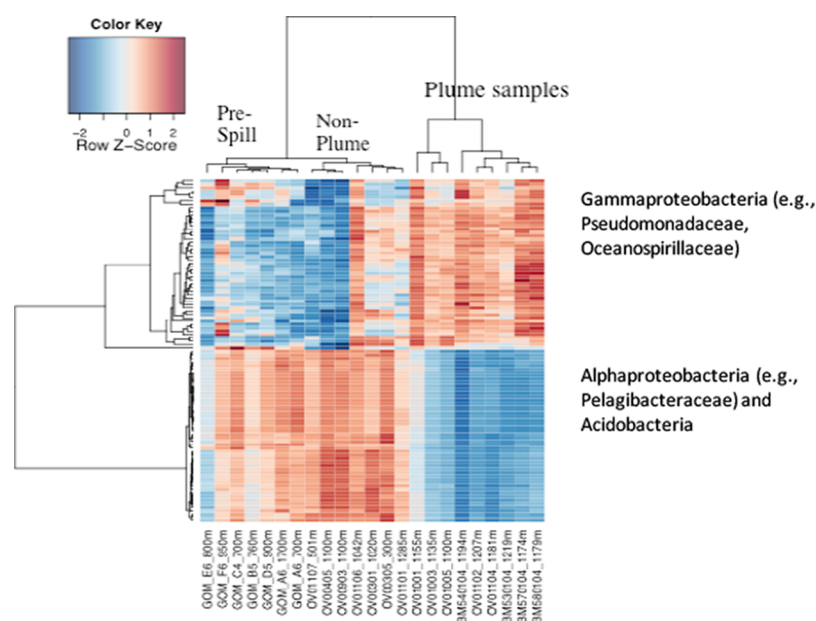
Figure 2. Microbial community in the deep-water plume was distinct from the microbial community in uncontaminated waters at the same depth. Hierarchical clustering identified similarities between microbial communities. Uncontaminated deep-water samples showed a higher relative abundance of *Alphaproteobacteria* and *Acidobacteria*, whereas the deep-water−oil plume had lower abundance of Alphaproteobacteria and Pelagibacteraceae and much higher abundance of *Gammaproteobacteria* including *Oceanospirillaceae* and *Pseudomonadaceae*.

2.2. Dynamics of Microbial Community Succession in Response to Oil.

The complex composition of crude oil is matched by a complex community of microbes that degrade it, and this community changes as biodegradation proceeds. As the preferred substrates are consumed the microbes specialized to consume those compounds die off and are replaced by microbes able to utilize the remaining compounds, a process of bloom and succession that was observed during the *Deepwater Horizon* spill (Figure 3).[28] During the initial phase of the spill, which began on April 20, 2010, the microbial community was dominated by *Oceanospirillales* able to consume a variety of alkanes.[26,33] Starting on June 4, 2010, there was a shift in the
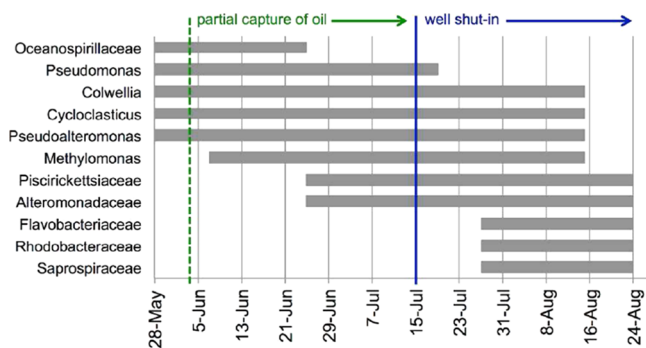
Figure 3. Succession of the microbial community in the deep water of the Gulf of Mexico during the various phases of the response to the *Deepwater Horizon* oil spill. For each bar relative abundance was enriched over background in any sample (>2-fold mean nonplume intensity).[43]

microbial community to dominance by *Colwellia* and *Cyclo-clasticus*. *Colwellia* was shown to consume propane, ethane and butane[27] and *Cycloclasticus* was shown to consume BTEX (benzene, toluene, ethylbenzene, and xylenes) as well as some PAHs. Finally, after well shut in, the microbial community shifted to dominance by Flavobacteria (*Tenacibaculum* and *Polaribacter*), *Alteromonadaceae,* and *Rhodobacteraceae*.[28] These groups are often found as degraders of high molecular weight organics and dissolved organic matter in the marine environment. This suggests that after well shut in the microbial community shifted to grow off the organic matter released from the decaying bloom of hydrocarbon degraders. These shifts underscore the dynamic nature of the microbial response to released oil. Degradation of a complex contaminant, such as oil, necessitates a complex microbial community response.

3. CRITICAL BIOGEOCHEMISTRY

The intrusion of oil into a marine system provides a substantial surplus of carbon for microbial growth. However, low availability of nutrients such as nitrogen and phosphorus can limit microbial growth and thus oil degradation. The addition of fertilizers containing bioavailable nitrogen and phosphorus has been successfully used to enhance oil biodegradation on a number of different shorelines[34] including the Arctic.[35] The *Exxon Valdez* oil spill has been the most studied in this regard. Approximately 50 000 kg of nitrogen and 5 000 kg of phosphorus were applied to shorelines in Prince William Sound over a three-year period.[36] Extensive laboratory and field-testing found that the addition of nutrients stimulated the growth of hydrocarbon-degrading microorganisms thereby increasing the observed rate of oil degradation.[37]

Following the *Deepwater Horizon* oil spill, a rapid enrichment of hydrocarbon-degrading microorganisms was observed in the water column, and surface and subsurface plume waters were dominated by known hydrocarbon-degrading bacteria.[38] Perhaps because substrate availability was limited as the surface slicks coalesced into thick emulsified oil with much reduced surface area for microbial colonization, Edwards et al.[39] found no increase in microbial biomass in the surface slick and that microorganisms exhibited enzymatic signs of phosphate stress consistent with previous observations that the Gulf of Mexico is limited by phosphate availability. Hazen et al.[26] found that microbial cell density in the deep water−oil plume was significantly higher than waters outside of the plume; > 5.5 × 10^4 cells/ml in the oil plume and <2.7 × 10^4 cells/mL outside

of the plume, but the increase was not as dramatic as might have been expected. This is likely due to the low concentrations of oil in the deepwater plume (<1 ppm). We note that the Gulf of Mexico has similar levels of nitrogen and phosphorus to several other marine environments undergoing active oil and gas exploration, but other areas, such as the Eastern Mediterranean Sea, have a much lower phosphorus level. If a spill were to occur in this environment, the rates and extent of biodegradation may be initially much slower than in the Gulf of Mexico. On the other hand, as dispersed oil continues to dilute as it gets further from a spill site, it is likely that eventually the oil to available nutrient ratio will drop to a value where biodegradation can proceed to completion.

Microbial degradation of hydrocarbons is often an oxidative process where the initial attack is performed by oxygenases and peroxidases. Aerobic conditions are thus necessary for degradation to occur through these pathways. Surface waters are rarely oxygen limited, but oxygen concentrations can decrease throughout the water column and under some circumstances there can be anoxic conditions in bottom waters. Further, sediments are usually anoxic a short distance below the surface, although in some cases oxygen penetrates many meters below the seabed.[40] Thus, it is unlikely that oxygen will limit biodegradation of surface slicks or in the upper levels of the water column. Oxygen limitations may occur at lower depths depending on the concentration of oil and the rate of oxygen replenishment by waves and currents; however, since oil droplets dilute quickly, it is unlikely that oxygen will become depleted in the water column. Degradation of hydrocarbons in the absence of oxygen has been shown to occur in the presence of other electron acceptors such as Fe^{3+}, SO_4^{2-} and NO_3^{-}.[41] Anaerobic degradation of hydrocarbons is usually considered to be several orders of magnitude slower and less is known about the genes and enzymes involved in these pathways.[42] Marine harbor sediments have been shown to degrade petroleum hydrocarbons under anaerobic conditions and specifically under sulfate-reducing and iron-reducing conditions.[43] Some marine environments such as the Caspian Sea have permanent anoxic conditions in bottom waters, so any biodegradation occurring there must be anaerobic, perhaps sulfate-reducing.

4. ROLE OF SYNERGISTIC EFFECTS IN OIL DEGRADATION

As we have discussed, the fate of oil in marine systems is dependent on a number of physical, chemical, and biological factors working independently or in consort with one another. The most important seems to be the physical state of the oil, and this can be altered by adding dispersants—mixtures of surfactants designed to lower the interfacial tension of oil and water so that even minimal turbulence can generate tiny droplets.[44−46] It has long been assumed that since dispersants encourage smaller droplets they would stimulate biodegradation because the surface to volume ratio would favor attachment and subsequent degradation.[46] One difficulty in testing this has been creating oil droplets of uniform and different sizes, and keeping them in suspension in seawater in the laboratory. Recently Brakstad et al.[45] demonstrated with a unique apparatus, and low concentrations of oil typical of a dispersed plume −3 ppm oil, that 10 μm oil droplets degrade faster than 30 μm oil droplets over 70 days using Macondo oil from the *Deepwater Horizon*. Droplets degrade much faster than surface slicks,[46] and there are now a number of studies reporting very rapid biodegradation of dispersed oil.[47]
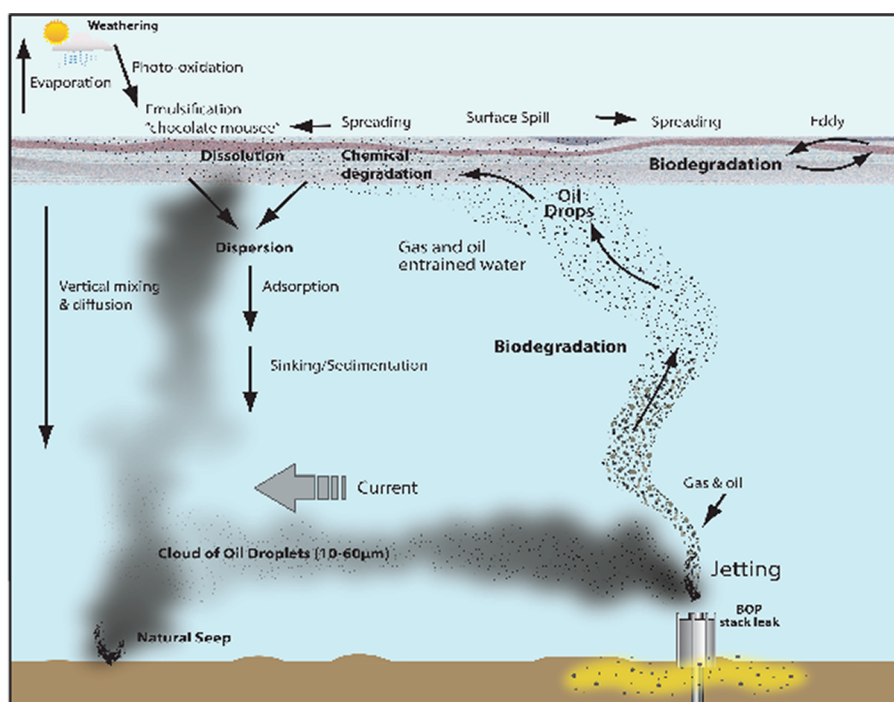
Figure 4. Fate of oil spills in marine environment (BOP = BlowOut Prevention device).[25]

Dispersants were used at a wellhead for the first time during the *Deepwater Horizon* oil spill, injected at a rate of 40 Lm^{-1} for a total of 3 million L in the deep injection.[48] Another 4 million L of dispersant were sprayed on the surface slicks during the response phase. According to the Operational Science Advisory Team,[48] dispersant components were not found in either the deep or surface water samples collected away from the wellhead. Nevertheless, Kujawinski et al.[49] demonstrated that one component, dioctylsulfosuccinate (DOSS) could be detected with sensitive LC/MS/MS techniques up to 64 days after the deep-water injections ceased, although it was noted that since the compound is used in a myriad of consumer and industrial products, it is found in many environments and could have been from other sources.[49] Hayworth et al.[50] concluded that traces of dispersant components found nearshore were from stormwater discharges, not dispersant application.

Other vital factors include environmental conditions (e.g., dissolved oxygen, water temperature), physical conditions of the system (e.g., currents, eddies, waves), diffusion of oil in the water column, and the microbial diversity and function within the water column. For example, Li et al.[51] showed that both chemical dispersants and mineral fines each resulted in an increase of oil dispersion, and when combined the formation and transport of oil droplets and oil−mineral aggregates from the surface to the water column increased significantly. Figure 4 illustrates what is believed to have happened to the rising oil droplets and the deep-water plume (<1 ppm total petroleum hydrocarbons) that was created by the jetting of the oil into the deep and the application of dispersant at the Macondo wellhead.

5. TRANSPORT OF HYDROCARBONS BY OCEAN CURRENTS

Until recently, the synergistic role of oceanic currents and gyres affecting oil biodegradation was not well documented, although the impacts of waves and mixing had been studied within wave

tanks and simulation models.[51] During the *Deepwater Horizon* oil spill, Valentine et al.[52] were able to model the effect of transport on microbial community structure and hydrocarbon biodegradation within the deep plume in the Gulf of Mexico. Specifically, the model was designed to track mixing of deep waters, circulation of water within the Gulf of Mexico, fluxes in bacterial abundance and metabolic rates, and hydrocarbon degradation rates. In total 26 compounds and 52 microorganisms were incorporated into the model design[52] and it suggested that autoinoculation and "memory response" were key components that enhanced biodegradation rates. Autoinoculation occurs when hydrocarbons moving in the water are mixed with previously exposed water parcels containing hydrocarbon-degrading microorganisms. Memory response is the ability of previously exposed microorganisms to degrade at a significantly faster rate than during initial exposure.

One autoinoculation event is predicted as occurring in mid-June until mid-July 2010, when waters from the Northwest region returned to the Macondo wellhead and remained there until the discharge was terminated.

6. COMETABOLIC BIODEGRADATION OF OIL

Studies by our group[26] and others[53,54] established that the deep oil cloud (<1 ppm total petroleum hydrocarbons), which developed as small droplets were released from the *Deepwater Horizon* wellhead, was rapidly dispersed and biodegraded. Though this deep-water plume could be seen spectrophotometrically, plume samples could not be identified by sight or smell by the scientists on board the sampling ships, except extremely close to the well head. The high rates of biodegradation of the Macondo oil were in part due to its being a light crude, which meant that a larger proportion of this oil was more inherently biodegradable. In terms of mass, the Macondo release was 38% natural gas and 62% liquid oil.[55] As we discussed above, the oil in the water column underwent progressive biodegradation by dominant microbial commun-

Table 2. Impact of Synergistic Effects on Biodegradation in Marine Systems

factor working synergistically	impact on biodegradation
Chemical dispersants + mineral fines.	Individually each will promote dispersion of the oil. Combined, the formation and transfer of oil from the surface into the water column is enhanced.[51]
Autoinoculation + 'memory response" of hydrocarbon degraders.	Introduction of hydrocarbons to previously exposed water parcels leads to an increase in microbial abundance and accelerated hydrocarbon biodegradation.[52]
Oil droplet size + dispersion + biodegradation rates + dissolution.	Enhances biodegradation, dissolution and dispersion rates of oil hydrocarbons.[45]
Cometabolic biodegradation + dispersion + secondary electron donors.	Enhances biodegradation, dissolution and dispersion rates of oil hydrocarbons even when the oil itself cannot be a suitable electron donor.[56]
Biosurfactants from multiple microorganisms.	Enhances bioavailability of poorly soluble compounds.[70,71]

ities as the more readily degradable components gave way to the more recalcitrant ones. Methane was degraded after most of the light liquid components had been degraded or diluted to very low concentrations. Indeed, in August and September 2010, when oil in the water column was barely detectable, the biodegradation of methane by methane-oxidizers surged to create some detectable dissolved oxygen dips in the water column.[53]

Cometabolism may well be an important process for removing oil components. Cometabolism is the process by which a contaminant is fortuitously degraded by an enzyme or cofactor during microbial metabolism of another compound. Typically, there is no apparent benefit to the microorganism involved, but it enables biodegradation of contaminants at concentrations that are below the concentration that could be of carbon or energy benefit to the biodegrader. Thus, cometabolic bioremediation has the added advantage of allowing scrubbing of environmental contaminants to un-detectable concentrations, for example, < parts per trillion. Cometabolic bioremediation has been applied both aerobically and anaerobically to a wide variety of contaminants in different environments. It has now been used in the field for more than 20 years on some of the most recalcitrant contaminants (e.g., halogenated aliphatic and aromatic hydrocarbons, explosives, dioxanes, creosote, crude oil, and pesticides).[56]

Many aerobic cometabolic biodegraders are dependent upon oxygenases, for example, methane monooxygenase, toluene dioxygenase, toluene monooxygenase, and ammonia mono-oxygense. These enzymes are extremely strong oxidizers (e.g., methane monooxygenase is known to degrade over 300 different compounds).[57] However, like any bioremediation process the proper biogeochemical conditions are necessary to maximize and maintain biodegradation (e.g., maintaining oxygen levels, nutrients or other terminal electron acceptors that the cometabolic biodegrader is dependent on). In addition, cometabolic biostimulation may require pulsing of electron donor or electron acceptor to reduce competitive inhibition between the substrate the microbe can use and the contaminant. Pulsing of methane was found to significantly improve biodegradation of trichloroethylene (TCE), creosote and oil rates by methanotrophs. Recent reports suggest that methane may have persisted in the Gulf of Mexico beyond initial reports.[53] Crespo-Medina et al.[58] showed that although gas-rich deep-water plumes were a short-lived feature initially, water column concentrations of methane remained above background levels throughout the rest of the year. Rates of microbial methane oxidation peaked in the deep-water plumes in May and early June, coincident with a rapid rise in the abundance of known and new methane-oxidizing microbes.[58]

It seems likely that a number of factors can work synergistically to affect the biodegradation of oil with unforeseen outcomes in marine systems (Table 2). Thus, a systems approach should be included in planning for oil spill mitigation.

7. SUMMARY AND FUTURE RESEARCH DIRECTIONS

Microorganisms that can degrade oil are in all marine environments, even cold, deep (low nutrient), and high-pressure settings. The number of taxonomically identified oil-degraders is increasing exponentially. However, even though the same groups of microorganisms are found in deep-sea, near-shore and sediments worldwide, the rates at which they degrade oil may vary significantly. Exposure to natural seeps and recent anthropogenic oil spills likely increases the biodegradation rates of oil. Marine half-lives of dispersed oil can range from 1 day to months; however, in the deep-sea it is more common to see half-lives of days or weeks. Even in pristine environments, the microbial community can rapidly shift to oil biodegradation because similar compounds are naturally found in the environment. Undispersed oil is likely to have a much longer lifetime in the environment, because the surface area available for microbial attachment is much less, and competing physical processes, especially photo-oxidation, likely interfere with biodegradation. A further complicating factor might be the overall limiting nutrients (P, N, Fe) and other physical/ chemical characteristics of the environment including currents, pressure, temperature, etc., which might select for different hydrocarbon-degrading organisms. In marine environments, oxygen limitations are rare due to the low concentrations of oil caused by natural and chemical dispersion which limits the relative oil concentrations in the water column to <1 ppm. The overall impacts on biodegradation from synergistic effects of chemical additives, biosurfactants, and autoinoculation of water parcels may be significant. As such, it is important to consider the role of multiple factors, including those outlined above, when developing remediation strategies and evaluating the fate of oil within marine systems.

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Notes
The authors declare no competing financial interest.

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