Chapter 18
Petroleum Microbiology Under Extreme Conditions

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Abstract Petroleum contamination of environmental matrices is a pervasive, global problem. Crude oil exploration, processing, handling and transport release significant amounts of petroleum hydrocarbons into the environment. Many petroleum compounds are known or suspected carcinogens, mutagens and teratogens and therefore, pose significant risks to human and ecosystem health. Petroleum hydrocarbon pollution constitutes an enormous challenge when areas with sub-optimal environmental conditions are contaminated. This is because these regions are characterized by the occurrence of delicate ecosystems and because remedial efforts tend to be frustrated, owing to the unfavourable climatic and environmental conditions. Due to extensive petroleum exploration in some of these areas, petroleum hydrocarbon contamination occurs frequently, degrading the environment. Efficacious, sustainable abatement strategies are therefore, necessary to mitigate contamination.

Over time, several treatment schemes and strategies for the replenishment of petroleum-contaminated sites have been designed, optimized and implemented. Many conventional techniques and technologies however, have significant limitations. This has prompted research into environmentally friendly and cost-effective clean-up alternatives. Bioremediation is an appealing option, which has been the subject of extensive research and has been adopted in many parts of the world because of its (comparative) low cost, minimal environmental impacts and public acceptance. Here, the general sources of petroleum hydrocarbons into the environment are explored as well as the effects of physicochemical and environmental factors on the transport, microbiology and overall fate of petroleum hydrocarbons in environmental matrices. The potential of petroleum hydrocarbon biodegradation under extreme environmental conditions is considered with an emphasis on the effects of unfavourable salinity, temperature, moisture, oxygen, nutrient, pressure and pH conditions. The roles of extremophiles in petroleum hydrocarbon biodegradation in extreme environments are also discussed. The influence of biosurfactants and the capacity of extremophiles to produce these under extreme environmental conditions are discussed as

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well as the relevance of bioaugmentation and biostimulation. Bioavailability, which influences the overall rate and efficiency of bioremediation protocols, is also considered.

18.1 Introduction

Petroleum is a heterogeneous mixture of simple and complex hydrocarbons (Atlas 1981). Petroleum hydrocarbons can be classified into the saturates or aliphatics (including n-alkanes, branched alkanes and cycloalkanes), the aromatics, the (polar) asphaltenes (phenols, fatty acids, ketones, esters and porphyrins) and the resins (pyridines, quinolines, carbazoles, sulphoxides and amides) (Atlas 1981; Leahy and Colwell 1990). Organometallo constituents such as vanadium and nickel as well as nitrogen, sulphur and oxygen in some amount may also be found occurring in petroleum (Van Hamme et al. 2003). The different constituents vary in physicochemical properties depending on the source and formation and based on relative proportions of heavy molecular weight constituents present, are classified as light, medium or heavy (Varjani 2017). Petroleum hydrocarbons and products (such as gasoline, kerosene, diesel) are introduced into the environment during offshore and onshore petroleum industrial activities including exploration, extraction, production, refining, transportation, processing and storage (Varjani 2017). Other anthropogenic sources include industrial and municipal discharges, accidental spills, incomplete combustion of fossil fuels and so on (Peixoto et al. 2011; Varjani 2017). Many of these compounds, particularly the high molecular weight ones, are hydrophobic, stable and therefore, recalcitrant, remaining in environmental matrices for protracted periods (Atlas 1981). They are also confirmed or potential carcinogens, mutagens and teratogens; thus they pose substantial health risks to humans and ecosystems (Varjani 2017).

Conventional approaches and strategies, including physical and chemical technologies, have been optimized and utilized to ameliorate petroleum contamination and restore polluted sites (Castaldini 2008). Drawbacks, such as technological complexity, high cost and a general lack of public acceptance, however, limit the efficacy of some of these. Many of the techniques are invasive and merely relocate the contamination problem, often requiring further management (Castaldini 2008). Experts reckon that it is more practical to adopt a sustainable approach that is cheaper and more environment friendly, which will completely mineralize the pollutants or transform them into innocuous substances (Lundstedt 2003; Castaldini 2008).

Bioremediation is a biological approach that is an appealing alternative because it has been demonstrated to be relatively cost-effective, environmentally friendly, generally accepted and in many documented cases, more effective (Bamforth and Singleton 2005). Environmental factors such as temperature, pH, moisture, salinity and pressure are pivotal in the removal of petroleum hydrocarbons from contaminated sites (Martínez Álvarez et al. 2017). Other relevant factors include the scale of pollution (e.g. the volume of oil spilled), characteristics of the impacted area, duration of the contamination (spills), financial circumstances, perceived risks and regulatory stipulations (Filler et al. 2008).

18.2 The Effects of Physicochemical Characteristics on Microbiology of Petroleum Hydrocarbons

The composition of discharged petroleum hydrocarbons varies significantly, depending on the source, generation mechanisms, weathering of the product over time, differential movement of the components in the environment (or migration) as well as trapping and possible alteration (Heath et al. 1993; Head et al. 2003). Physicochemical properties differ depending on the constituent and percentage or concentration of crude or refined oil that is spilled (Speight and El-Gendy 2018d). Variations in composition and properties among different crude oil constituents and refined products influence the rate of biodegradation of oil and its component fractions (Leahy and Colwell 1990). There are different constituents of petroleum with varying molecular structures – could be straight or branched chain, single or condensed rings or aromatic rings (Speight and El-Gendy 2018a). Some common constituents include alcohol, ether, simple alkanes/alkenes, cycloalkanes, chlorinated aliphatics, ethyl alkanes/alkenes, monocyclic aromatic hydrocarbons [such as benzene, toluene, ethylbenzene and xylene (BTEX)] and polycyclic aromatic hydrocarbons (e.g. anthracene, phenanthrene and benzo(a)pyrene) (Atlas 1981). Physicochemical properties differ – molecular weight, water solubility, specific gravity, vapour pressure, diffusivity, organic carbon/water partition coefficient, octanol/water partition coefficient, marine life bioconcentration/bioaccumulation factors, biota-sediment accumulation potential and surface water half-life. These factors influence their transport and fate in environmental matrices (Van Stempvoort and Biggar 2008). Susceptibility to microbial attack differs considerably among hydrocarbons depending on molecular weight and structure. The HMW compounds are generally more hydrophobic (Bamforth and Singleton 2005). Hydrocarbons ranging from C_{10} to C_{26} and LMW aromatics are usually more readily degraded (Atlas 1995), whereas more complex compounds such as those comprising of fused aromatic (benzene) rings as well as a system of hydrophobic and lipophilic double bonds in their structures are generally more resistant to biodegradation (Van Stempvoort and Biggar 2008). Biodegradability of oil components generally decreases in the following order: n-alkanes, branched-chain alkanes, branched alkenes, low molecular weight n-alkenes, aromatics, monoaromatics, cyclic alkanes, PAHs and asphaltenes (Schmidt and Schaechter 2012). Biodegradation rates are highest for unsaturated compounds, followed by the light aromatics, with high molecular aromatics and polar compounds (asphaltenes and resins) exhibiting low rates of degradation (Oudot 1984; Chandra et al. 2013). For example, aliphatic compounds, which are less hydrophobic, are more prone to degradation compared to polycyclic aromatic hydrocarbons, which are not only more hydrophobic but also have higher sorption capacity (Haritash and Kaushik 2009). Also, it is apparent that abiotic losses of lighter oils are higher compared to heavier oils. They are also more susceptible to biodegradation compared to heavier oils (Atlas 1995).

Solubility affects constituent migration in surface water, soils and groundwater (Lu et al. 2012). Similarly, volatility influences the mobility and recalcitrance of organic and inorganic constituents. Vapour pressure and solubility affect constituents' volatilization potential or ability to partition from the aqueous phase to the vapour phase. All of these factors have direct impacts on the adsorption capacity – potential to adsorb to soil organic matter or sediment particulate matter (Atlas 1981). These directly influence migration through contaminated matrices such as soil and aquifer as well as migration (or partitioning) from surface water to sediments, bioavailability and overall fate and transport of petroleum hydrocarbons both near and far from the original point of release in the environment (Atlas 1981). These factors also influence the overall toxicity of the oil, the consequent deleterious effects on the indigenous microbial community as well as the toxicity that reaches human and ecological receptors (Atlas 1981).

18.3 Fate of Petroleum Hydrocarbons in the Environment

Some of the likely processes and pathways, to which released petroleum hydrocarbons may be subjected to, include volatilization, photo-oxidation, chemical oxidation, emulsification, adsorption onto particulate/organic matter, leaching and microbial degradation (Wild and Jones 1995; Pantsyrnaya et al. 2011). Major pathways of petroleum hydrocarbons in the aquatic environment include dissolution, adsorption onto suspended solids and subsequent sedimentation, biotic and abiotic degradation, uptake by aquatic organisms and accumulation (Pantsyrnaya et al. 2011). These processes and pathways are ultimately responsible for or contribute to their removal.

Petroleum contamination of terrestrial and aquatic ecosystems is quite common (Logeshwaran et al. 2018). There are, however, key differences in remediation in these different ecosystems. The main issues are related to the spreading and movement of the oil as well as the incidence of particulate/organic matter, which significantly influences the behaviour of the pollutants and therefore, its susceptibility to and rate and efficiency of microbial degradation (Leahy and Colwell 1990). Dispersion of hydrocarbons in the water column in the form of oil-in-water emulsions increases the surface area of the oil and thus its availability for microbial attack. This improved dispersion and emulsification enhances degradation rates in aquatic ecosystems, whereas the potential for adsorption to particulates in terrestrial ecosystems has negative implications for the efficacy of degradation (Leahy and Colwell 1990; John and Okpokwasili 2012). In the case of terrestrial oil spills, the oil typically moves vertically into the soil as opposed to horizontal distribution associated with slick formation (Leahy and Colwell 1990). Percolation of oil into the soil minimizes evaporative losses of volatile hydrocarbons, which can be toxic to microorganisms (Sherry et al. 2014). Particulate matter can reduce, by absorption, the effective toxicity of the constituents of petroleum, but absorption and adsorption of hydrocarbons to humic substances probably contribute to the formation of persistent residues (Leahy and Colwell 1990). The chemical structure of the hydrocarbons also matters, because generally, the higher molecular weight compounds are more hydrophobic and toxic and persist longer in environmental matrices (Bamforth and Singleton 2005).

The remediation strategies designed to ameliorate petroleum hydrocarbon pollution are generally classified into three main categories including physical (e.g. excavation, retrieval and off-site disposal, dredging, dry excavation of sediments, thermal treatment, capping technique and incineration), chemical (chemical oxidation, photocatalysis and solvent extraction, amongst others) and biological (bioremediation – transformation and mineralization) (Singh 2006). Physical treatment systems may be used in conjunction with attenuation approaches or in the case of polluted groundwater, can take the form of permeable reactive barriers that transform pollutants into environmentally acceptable forms (Tong and Yuan 2012).

Some common traditional oil spill clean-up techniques include the use of controlled burns, skimmers, vacuum pumping, low pressure flush, other manual mechanical techniques and the use of gelling agents, amongst others. These techniques will however, merely relocate the contaminants from the impacted environment to a different location or create further pollution (Castaldini 2008). Expensive, complicated technology, energy inefficiency and general public scepticism are other significant limitations of available conventional techniques (Castaldini 2008). It is more sensible to adopt protocols that are not only effective but also more environmentally sound and sustainable.

Bioremediation harnesses the biodegradative capabilities of living organisms to either completely destroy petroleum hydrocarbons or transform them into harmless forms (Vidali 2001; Lundstedt 2003; Castaldini 2008). It uses living organisms, including plants, animals but primarily microorganisms, to remove or neutralize petroleum contaminants (Barret et al. 2010; Langenbach 2013). This could be via the adoption of a natural degradation pathway or through the stimulation (and optimization) of recombinant strains to use hydrocarbons as carbon or energy sources (Lu et al. 2012). Bioremediation can occur on its own through natural attenuation (intrinsic bioremediation) but in most cases could take a long time (Brown et al. 2017). As such, various bioremediation strategies have been developed to promote the microbial metabolism of contaminants by manipulating several variables (Langenbach 2013). Some of these strategies include biostimulation (stimulating viable native microbial population), bioaugmentation (artificial introduction of viable populations), biosorption (dead microbial biomass), bioaccumulation (live cells), phytoremediation (plants) as well as rhizoremediation (plant and microbe interaction) (Sharma 2012). Other common examples of bioremediation technologies are land farming, bioventing, bioleaching, composting and the use of bioreactors amongst others (Vidali 2001; Chadrankant and Shwetha 2011). Laboratory and field trials, documenting successful reduction of petroleum contaminant levels, abound in the literature. In situ and ex situ applications have been optimized, and all of these have proven that bioremediation technologies are not invasive, are energy efficient and are eco-friendly (Sharma 2012; Castaldini 2008).

The rate, efficiency and overall success of petroleum hydrocarbon bioremediation depend on a variety of biotic and abiotic factors (Leahy and Colwell 1990). The presence and activity of efficient petroleum-degrading microbiota in the contaminated environment and their adaptive response to the presence of hydrocarbons, the physiological capabilities of these populations, and existing abiotic circumstances that may influence the growth and proliferation of the hydrocarbonoclastic strains (i.e. how conducive the environment is) affect the success of bioremediation efforts (Atlas 1981; Leahy and Colwell 1990; Chadrankant and Shwetha 2011). Ratios of various structural classes of hydrocarbons present, properties of the biological systems involved, competitiveness, degree of acclimation and accessibility of the contaminants are also crucial. The bioavailability of the substrate, cellular transport properties, concentration and accessibility of nutrients are equally important conditions (Van Hamme et al. 2003; Alegbeleye 2015).

Several life forms, capable of proficiently degrading various classes of hydrocarbons, have been characterized (Shukla et al. 2014). However, microorganisms are better candidates for bioremediation because of their ubiquitous distribution in normal and extreme environments, fast biomass growth, easy manipulation and high diversity of catabolic enzymes (Sharma 2012; Patil and Rao 2014). A myriad of prokaryotic and eukaryotic organisms are capable of metabolizing petroleum hydrocarbons, and these are dominated by *Eubacteria*, comprising 7 of the 24 current major phyla (Prince et al. 2010; Margesin 2017). Overall, site-specific circumstances can be highly variable and can have profound effects on the efficiency of selected treatment strategy (Prince et al. 2010). Extreme environmental conditions may constrain hydrocarbon degradation, rendering bioremediation in certain environments problematic (Van Hamme et al. 2003). Extreme, sporadic fluctuations and variations have been reported in some hydrocarbon-contaminated regions. In the Antarctic, for example, drastic temperature changes such as from −15 °C to nearly 30 °C within 3 h have been reported (Cowan and Tow 2004).

Isolation, identification and characterization of microorganisms capable of proficiently degrading the vast range of petroleum substrates/contaminants in locations with harsh environmental conditions has been recognized as fundamental and vital to the success of clean-up. Strategies, which maximize rates and efficiency of microbial growth and utilization of petroleum hydrocarbons under such peculiar environmental conditions, as well as improved microbial access for hydrocarbon contaminants, and transformations have been designed and optimized over the last several decades (Van Hamme et al. 2003). Members of bacteria, yeasts, fungi and algae have been isolated for these purposes (Buzzini and Margesin 2014; Maiangwa et al. 2015). The development of molecular tools and strategies has further enhanced our understanding of microbial community structure and hydrocarbonoclastic capacity (Varjani 2017). Numerous studies have explored and described genes, community composition, complexity of interactions, trophic levels, guilds, functional diversity, enzymes and transformation steps for some hydrocarbons both under ambient and extreme environmental conditions (Van Hamme et al. 2003). The biochemistry, genetics and pathways of hydrocarbon degradation have been provided in some cases (Bosch et al. 1999; Pinyakong et al. 2003; Liang et al. 2006; Sierra-García et al. 2014; Bian et al.

2015). Studies that have illustrated the hydrocarbon metabolic capacities of extremophilic microorganisms are available (Whyte et al. 1996; Abed et al. 2014). Typical microbial cellular and physiological responses to petroleum hydrocarbon pollutants such as cell surface alterations, adaptive mechanisms for accession and uptake and efflux of these substrates in optimal environmental conditions have been extensively explored; however, a lot remains unknown about metabolism of petroleum compounds in extreme environments (Van Hamme et al. 2003).

18.4 The Concept of Extremophiles and Their Implications for Bioremediation

Based on the characteristics of biomolecules and requirements for biochemical reactions, there are specific physicochemical limitations to cellular processes (Dion and Nautiyal 2007). There are maximum and minimum environmental requirements, above and below which it becomes very difficult for microorganisms to survive (Shelford 1913). Environmental conditions that are near limits for cell functioning are regarded as 'extreme', and these are typically damaging to biomolecules or limiting for enzyme activities (Torsvik and Øvreås 2008).

Extremophiles can be grouped according to the conditions to which they are adapted or thrive. They are classified as thermo (high temperature), psychro (low temperature), hyperthermo (very high temperatures), halo (high salt concentration), acido or alkali (extreme low or high pH), ero (low water activity) and baro (under pressure) (Torsvik and Øvreås 2008; Rampelotto 2013). The suffix -phile is used for those that thrive under the extreme conditions (require such for optimum metabolic activities) and troph or tolerant for those that tolerate the extreme condition (Torsvik and Øvreås 2008). In other words, extremophiles are adapted to and are limited by very narrow sets of environmental conditions, and they require the extreme conditions for their metabolic processes, whereas extremotrophic or extremotolerant organisms are more flexible as they can survive and proliferate under a wider set of environmental parameters. That is to say, they tolerate extreme environmental conditions but will ideally cope better under moderate 'normal' conditions (Rampelotto 2013).

A broader but less conventional definition includes organisms, which can tolerate pollution such as heavy metals, ionizing radiation and organic or other toxic compounds (Torsvik and Øvreås 2008). Research indicates that the taxonomic diversity of microbial populations in 'extreme' environments is low (Dong and Yu 2007). This is consistent with ecological principles related to biochemical requirements described previously that these extreme environments are inhabited by less diverse communities. However, many microbial species are stretching the boundaries for their life processes thereby evolving to at least subsist under these otherwise stressful conditions. Others have been documented to thrive and proliferate under these harsh conditions (Peeples 2014; Varshney et al. 2015). Many times, two or more extreme variables may prevail within the same environment as independent or interrelated conditions (Birch 2017). For instance, many hot springs are acidic and alkaline at the same time and usually have high metal concentrations; the deep ocean is generally cold, with oligotrophic (very low nutrient content) and high hydrostatic pressure conditions; and also, several hypersaline lakes are very alkaline (Glazier 2014; Fazi et al. 2017). Therefore, many extremophiles are normally poly-extremophiles, being adapted to survive in habitats with diverse extreme physico-chemical parameters (Torsvik and Øvreås 2008; Rampelotto 2013). In some areas such as the Antarctic deserts, several harsh environmental factors interact, such as low temperature, low annual precipitation and strong desiccating winds (Dion and Nautiyal 2007). For instance, extreme temperature occurs concomitantly with extreme water stress in the deserts in Antarctica although in some areas and during restricted periods melting snow may generate some water (Kennedy 1993; Dion and Nautiyal 2007).

An organism may therefore, belong to multiple categories and, for example, be considered as both psychro- and xerophile (Seckbach et al. 2013). Microorganisms adapted to more than one extreme variable have better potential for biological decontamination of extreme environments where a wide range of extreme conditions may prevail simultaneously (Margesin and Schinner 2001).

Petroleum contamination of extreme environments characterized by low or elevated temperature, too acidic or too alkaline pH and high salinity or high pressure has been widely documented (Darvishi et al. 2011; Fathepure 2014; Al-Sarawi et al. 2015; Logeshwaran et al. 2018). High-temperature soils, permafrost soils, the Arctic and Antarctic, rainforests, abyssal regions, marine ecosystems such as the deep sea muds and sediments, deep ocean hydrothermal vent systems, hot springs and muds, salt evaporation ponds, crystalline rocks, ancient sedimentary rocks, hypersaline lakes, dry deserts and many others are contaminated continuously or periodically by petroleum hydrocarbons (Margesin and Schinner 2001). Various life forms which inhabit specific environments based on their biotic and abiotic characteristics, adapt/survive and in fact thrive under these so-called extreme environmental circumstances can however, be found in these diverse environments (Peixoto et al. 2011). Although optimal microbiological processes cannot be guaranteed under these conditions (Fathepure 2014), many extremophiles have been reported to metabolize petroleum compounds in these environments.

18.5 Sources and Occurrence of Petroleum Hydrocarbons in Extreme Environments

Oil exploration and production activities in extreme environments pose risks from oil discharges, leaks or spills, by-products such as natural gas condensates, transport and storage of petroleum and petroleum-derived products and so on (Van Stempvoort and Biggar 2008; Brakstad 2008). Mining activities and chemical and metallurgic industries in close proximity to these regions represent major risks as well.

18.6 Effects of Petroleum Contamination on Microbial Biodiversity

Many petroleum hydrocarbons are recalcitrant, bioaccumulative and toxic to living organisms and ecosystems (Hong et al. 2014). Their occurrences in environmental matrices cause ecological disturbances and alter biodiversity (Mapelli et al. 2017). After contamination events, microbial diversity may be significantly altered owing to sensitivity to different classes of petroleum pollutants (Yang et al. 2009). Petroleum hydrocarbon pollution events have been seen to induce microbial succession in affected ecosystems, associated with HC composition and quantity, as well as the delicate nature of microbial existence (Beazley et al. 2012; Mapelli et al. 2017). Selective pressure on microbial communities subsequent to pollution incidents such as oil spills has been observed (Beazley et al. 2012). In pristine environments, hydrocarbonoclastic group may account for only about 0.1% of the microbial community but could make up 100% of the viable microbial diversity in an oil-polluted ecosystem (Yang et al. 2009). Post-spill (Deepwater Horizon) samples from the Gulf of Mexico near Mississippi (United States) contained mostly oil-degrading organisms resulting from a drastic decrease in diversity (Atlas and Hazen 2011). An initial surge in *Oceanospirillales* and Pseudomonads population (in May 2010), right after the spill, which occurred in April 2010, was observed. A shift in dominance to *Colwellia*, *Cycloclasticus*, *Pseudoalteromonas* and methylotrophs, which persisted until August 2010, was subsequently detected (Mapelli et al. 2017). The actual physiological drivers for the observed shift in microbial community remain controvertible; however, studies and reports have strongly associated this with the spill. Selective pressure exerted on microbial communities by the large increase of petroleum and other petroleum derivatives selects for the survival and proliferation of organisms that can use petroleum and derivatives as energy, electron and/or carbon sources (Beazley et al. 2012). To design appropriate remediation protocols, it is important to understand the impact of petroleum contamination on microbial diversity – the cooperation, competition and succession of microorganisms post oil spill.

18.7 Petroleum Microbiology Under Extreme Environmental Conditions

18.7.1 Salinity

There is a close correlation between osmotic stress and water stress because solutes have a remarkable effect on water activity (Dion and Nautiyal 2007). High salinity is common in restricted habitats, and affected ecosystems especially soils are usually characterized by uneven temporal and spatial water distribution (Dion and Nautiyal 2007). These fluctuations are stressors for microorganisms, as they have to simultaneously adapt to desiccation and high salt concentrations. High levels of petroleum hydrocarbons have been detected in many hypersaline habitats such as salt flats, natural saline lakes, oilfields, saline industrial effluents, estuaries, beaches, inland lakes, rockpools, desert rain pools, sabkhas, other kinds of salt marshes and so on. Some of these habitats are ubiquitous features of arid and semiarid regions of the world with high evaporation rates (Central Asia, the Arabian Peninsula and Australia) that have been subjected to extensive crude oil contamination (Fowler et al. 1993; Al-Mueini et al. 2007; Al-Mailem et al. 2013; Fathepure 2014). Oilfields are especially problematic because there are a significant number of them worldwide and the high salinity is caused by salty brackish (produced) water generated during oil and gas extraction (Fathepure 2014). Disposal or recycling is expensive and challenging because of high salt levels (about 1000–250,000 mg/l), presence of oil and grease, toxic chemicals, heavy metals as well as certain radioactive materials (Cuadros-Orellana et al. 2006; Bonfá et al. 2011), although there are significant advancements in disposal technology as >95% of all produced waters are reinjected these days, as opposed to the old practice of releasing to the surface (Kuwayama et al. 2013). However, many small-/moderate-scale operators continue to release substantial amounts of produced water into the environment especially accidentally such as via leaky tanks and flow lines. Moreover, inappropriate management in the past has created environmental problems that persist until now in certain regions (Varjani 2017).

Positive correlations between salinity and rates of hydrocarbon mineralization have been demonstrated by several studies (Kerr and Capone 1988; Leahy and Colwell 1990; Van Hamme et al. 2003; Qin et al. 2012). High salt concentrations can lead to low oxygen and hydrocarbon solubility, disrupt cell membrane function and microbial tertiary protein structure, denature enzymes and dehydrate cells, thereby limiting microbial metabolic rates (Whitehouse 1984; Dupraz and Visscher 2005; Pernetti and Palma 2005). Microbial species of the domains Archaea, Bacteria and Eucarya have been isolated and characterized, and their metabolic capacity to degrade a myriad of aliphatic and aromatic hydrocarbons under varying salt concentrations has been demonstrated (Oren et al. 1992; Margesin and Schinner 2001). Several studies have illustrated microbial capacity to use crude oil constituents as carbon sources under moderate- to slightly high-salinity environmental conditions (Díaz et al. 2000; Abed et al. 2006).

There are however, conflicting reports in literature regarding microbial metabolic rates and salt conditions. Some studies indicate that halophilic and halotolerant species are exclusively required for successful bioremediation in high-saline environments, for example, discussed by Fathepure (2014), while some others suggest that salinity does not significantly affect microbial hydrocarbon degradation rates (Kerr and Capone 1988). There are other indications that increased salinity may enhance hydrocarbon biodegradation (Díaz et al. 2000; Yang et al. 2000), while hypersalinity has been shown to reduce microbial metabolism of hydrocarbons (Dupraz and Visscher 2005). For example, hydrocarbon metabolism rates decreased with increasing levels of salinity (3.3–28.4%) in hypersaline evaporation ponds of the Great Salt Lake, Utah, United States (Ward and Brock 1978), and more efficient

PAH degradation in a medium containing 0% NaCl than in a 5% NaCl medium has been reported (Minai et al. 2012).

Halophilic and halotolerant microorganisms, which have very versatile metabolic capacities, have been identified (Oren 2011). Halophiles including prokaryotes and eukaryotes, oxygenic and anoxygenic phototrophs, aerobic heterotrophs, fermenters, denitrifiers, sulphate reducers, methanogens, heterotrophic and methanogenic Archaea, photosynthetic, lithotrophic and heterotrophic bacteria, as well as photosynthetic and heterotrophic eukaryotes have been documented in literature to degrade various types of hydrocarbons (Oren 2002, 2011). Extremely halophilic prokaryotes can tolerate very low water potential and thrive at saturated NaCl concentration (0.75a_w). Salt solubility and not cell physiology determines this limit (Dion and Nautiyal 2007). Bacterial diversity decreases with an increase in salinity compared to Archaeal groups which generally increase (Jiang et al. 2007; Valenzuela-Encinas et al. 2008); therefore, Archaea is usually more predominant in high-salinity environments (Maturrano et al. 2006). This may be due to their different salt tolerance capabilities. Most halophilic bacteria can survive at moderate-salinity conditions of up to 2.5 M salt concentrations (Ventosa et al. 1998), but halophilic Archaea can survive up to salt saturation (Oren 2008; Mirete et al. 2015). Due to the differences in salt requirements, halophilic bacteria and Archaea tend to occupy different salinity niches with the former being mostly predominant in low salinity and the latter being dominant in high-salinity environments (Oren 2013). A succession of proteobacterial groups due to salinity has been reported by Wu et al. (2006) who studied the bacterioplankton (free-living) community composition along a salinity gradient of high mountain lakes located on the Tibetan Plateau, China.

Halophilic and halotolerant microorganisms adopt strategies such as the accumulation of small molecules (osmolytes or compatible solutes) in the cytoplasm to counter external osmotic pressure (Kempf and Bremer 1998; Dion and Nautiyal 2007). This is known as organic-osmolyte strategy, and it involves the accumulation of organic compatible solutes – zwitterions (e.g. proline, glycine betaine, ectoine, methylamines and derivatives) or nonionic molecules (polyols, carbohydrates, neutral peptides, as well as amino acids and derivatives) (Dion and Nautiyal 2007). This process is compatible since there is no actual need for the change of intracellular proteins and is quite common among the domain Bacteria and Eukarya and some methanogenic Archaea. Some other halophiles and halotolerant species maintain an osmotic balance by accumulating high salt concentrations via a strategy known as 'salt-in-cytoplasm strategy', but this requires salt adaptation of the intracellular enzymatic machinery and is therefore, energetically demanding (Oren et al. 1992). A minority of the known halophiles, including Halobacteriales of the domain Archaea and Halanaerobiales of the domain Bacteria, use this mechanism. Eubacteria's intracellular salt concentration is low, and the enzymes involved in biodegradation may be conventional (i.e. not salt dependent), and this confers an advantage on this group compared to Archaea (Oren et al. 1992).

Members of genera *Cellulomonas*, *Bacillus*, *Dietzia*, *Halomonas*, *Haloarcula*, *Haloferax*, *Halobacterium*, *Alcanivorax*, *Marinobacter*, *Streptomyces*, *Rhodococcus*, *Gordonia* and *Pseudomonas* are very popular in the literature (Huu et al. 1999;

Zvyagintseva et al. 2001; Wang et al. 2007; Mnif et al. 2009; Fathepure 2014). Some of these microorganisms have been isolated from environments with high salt concentrations such as the Cormorant oilfields in the North Sea, sediments associated with mangrove roots, oilfields, production water, oil and stratal waters and other saline environments (Borzenkov et al. 2006). These microorganisms have been reported to degrade aliphatic and aromatic crude oil hydrocarbons under salinity conditions ranging from 0 to as high as 30% NaCl (Díaz et al. 2000).

Specific examples of studies include microorganisms isolated from Argentine saline soils which were demonstrated to biodegrade diesel fuel (Riis et al. 2003). The degradation of hydrocarbons, crude oil, diesel oil, naphthalene, hexadecane, pyrene, dibenzothiophene, salicylate, catechol and phenanthrene as sole sources of carbon in a 0–10% salinity treatment medium by a *Bacillus* strain has also been documented (Kumar et al. 2007). An actinomycete, *Amycolicicoccus subflavus*, isolated from an oily sludge at Daqing oilfield in China degraded crude oil in the presence of 1–12% NaCl (Wang et al. 2010). Its genetic capacity to metabolize short-chain and long-chain *n*-alkanes like propane and C_{10}–C_{36} alkanes as sole carbon sources was subsequently demonstrated (Nie et al. 2013). *Marinobacter sedimentalis* and *M. falvimaris* have been isolated from soil and pond water collected from hypersaline sabkhas [coastal salt marshes (18–20% salinity)] in Kuwait (Al-Mailem et al. 2013). *Pseudomonas* sp. strain C450R and *Halomonas* sp. strain C2SS100 degraded 93–96% of the aliphatic fraction of crude oil (C_{13}–C_{29}), while producing biosurfactants in the presence of 5–10% NaCl (Mnif et al. 2011). Extreme halophiles that require at least 1 M NaCl (approximately 6% w/v) for survival and can grow optimally at NaCl concentrations above 3 M have been identified and described (Kushner 1978).

Other recent studies seem to place the optimum salinity requirements at neutral. The degradation rates of several hydrocarbons under a range of salinities 0, 35, 50, 80, 120 and 160 $g.L^{-1}$ were assessed by Abed et al. (2006). Microbial mats from an Arabian Gulf area chronically exposed to oil spills were investigated, and almost 100% of initial phenanthrene and dibenzothiophene were degraded at 35 $g.L^{-1}$. The best degradation results for pristine (approximately 75%) and n-octadecane (around 85%) occurred between salinities of 35 and 80 $g.L^{-1}$. Another study reported a 30% increase in degradation rate of petroleum hydrocarbons with a decrease in salinity from 2.86% to 0.10% (Díaz et al. 2002). Hydrocarbon biodegradation capacity of a mangrove microbial consortium immobilized onto polypropylene fibres with treatment salinity ranging from 0 to 180 $g\ L^{-1}$ was assessed by Díaz et al. (2002). Less than 40% alkane biodegradation was achieved in the 0 $g.L^{-1}$ NaCl medium, about 50% at 20 $g.L^{-1}$ and 65% at 40 $g.L^{-1}$. At higher salt concentrations (60–140 $g.L^{-1}$), alkane biodegradation rates were between 50–60% and reduced to less than 30% at 180 $g.L^{-1}$.

To bioremediate high-salt environments where there are no proficient halophilic or halotolerant strains, there are two possible strategies to override salinity. One is reducing the salt concentrations by dilution or irrigation with fresh water or diluted seawater to lower the salinity or the removal of salt by reverse osmosis, ion exchange or electrodialysis. The other is manipulating the bacterial species to function in a high salt concentration matrix (Oren et al. 1992; Rhykerd et al. 1995) by producing genetically engineered halophilic oil-degrading bacteria (Kapley et al. 1999), bioaugmentation with foreign consortia or stimulating metabolic/biochemical activity of indigenous species (biostimulation) (Al-Hadhrami et al. 1996). Although expensive, successful bioremediation of extreme environments has been achieved using these strategies. For example, the irrigation of polluted sediments in Kuwait, even though it altered microbial community, facilitated hydrocarbon bioremediation (Radwan et al. 1995; Al-Daher et al. 1998; Balba et al. 1998). Due to the cost implications of diluting high salt concentrations, the use of halophilic or halotolerant organisms seems to be a more promising option.

18.7.2 Temperature

Temperature significantly influences the rate and efficiency of petroleum hydrocarbon biodegradation (Atlas 1981). It has a marked influence on the diversity, physiology and metabolic capacity of microorganisms as well as the physicochemical characteristics (such as viscosity and solubility) of the hydrocarbons (Leahy and Colwell 1990; Foght and McFarlane 1999; Margesin and Schinner 2001). Seasonal shifts in the composition of microbial communities which affected hydrocarbon metabolism rates and efficiency at various temperature values have been reported (Atlas 1981). Temperature directly influences the solubility of many petroleum hydrocarbons, which dictates the degree of spreading and partly determines the surface area of oil available for colonization by hydrocarbon-degrading microorganisms (Yang et al. 2009). An increase in temperature leads to increased solubility, which in turn improves the bioavailability and mass transfer of the hydrocarbon substrates to microbial cells. There are, however, certain exceptions to this principle; for example, some small alkane constituents of petroleum oil are more soluble at 0 °C than at 25 °C (Polak and Lu 1973). Temperature influences solubility of oxygen, which decreases with increasing temperature and reduces the metabolic activities of aerobic species. It also influences availability of nutrients and other electron acceptors (Margesin 2017). It affects the equilibrium (partitioning) and kinetic rate constraints as illustrated by van't Hoff Isochore and Arrhenius equations, respectively. In addition, it influences the rate of abiotic losses such as through evaporation, volatilization, dispersion and oxidation (Atlas 1981). For example, in hot environments, volatile hydrocarbon fractions of crude oil have been observed to evaporate rapidly, leaving longer-chain aliphatic and aromatic constituents, which are generally more hydrophobic and persistent (Abed et al. 2006), although, in some cases, these volatile fractions were characterized as toxic and evaporated slowly, inhibiting microbial degradation of these oils at elevated temperatures (Atlas 1975, 1981; Floodgate 1984; Ubalua 2011).

At low temperatures, there is increased oil viscosity and the volatilization of short-chain alkanes is reduced, water solubility is reduced, and these may delay the onset of biodegradation as these conditions are typically not optimal to trigger biodegradation (Leahy and Colwell 1990; Atlas 1991; Margesin and Schinner 2001). Rates of degradation are generally observed to decrease with decreasing temperature, and this has been attributed to decreased enzymatic activity, or the 'Q_{10}' effect (Atlas and Bartha 1972; Gibbs et al. 1975). Higher temperatures increase the rates of hydrocarbon metabolism, with optimal mineralization typically in the range of 30–40 °C, above which toxicity of hydrocarbons to microbial cell membrane likely increases (Leahy and Colwell 1990).

Hydrocarbon biodegradation has been shown to occur over a wide range of temperatures, and psychrophilic, mesophilic and thermophilic hydrocarbon-utilizing microorganisms have been isolated and characterized (Atlas 1981; Margesin and Schinner 2001). It is however, noteworthy that a more abundant diversity of hydrocarbonoclastic microorganisms is prevalent at temperatures between 25 and 30 °C (Olliver and Magot 2005). Price and Sowers (2004) assessed the relationship between temperature and metabolic rates in different environments. Three categories of metabolic rates were distinguished: (a) rates sufficiently high to permit growth, (b) intermediate rates sufficient for maintenance of cell functions, but too low for growth, and (c) basal rates sufficient for cell survival as well as repair of damaged macromolecules, but otherwise permitting only cell dormancy. Minimum temperature required for metabolism was not established, but at low temperatures, extremely low metabolic rates were observed.

The effects of temperature are interactive with other factors such as the hydrocarbon composition of a petroleum mixture and the composition of the microbial community (Atlas 1981). For example, hydrocarbons such as isoprenoids, phytanes and pristanes seem to be generally more resistant to bacterial attack at low temperature (Atlas 1991).

18.7.3 Oxygen

Oxygen is an important, rate-limiting factor in bioremediation (Atlas 1995). It is a terminal electron acceptor for aerobic microorganisms and therefore, aids microbial growth (Logeshwaran et al. 2018). A good number of documented microbial degraders are aerobic, many of which have been demonstrated to decompose petroleum hydrocarbons, form biofilms and produce biosurfactants, slime and other biomolecules that aid pollution metabolism. In the major hydrocarbon degradation pathways, oxygenases and molecular oxygen are important participants (Aydin et al. 2017). Aerobic processes mostly generate a considerably greater potential energy yield per unit of substrate and tend to occur appreciably more rapidly (Yang et al. 2009). Moreover, most of the fully optimized bioremediation strategies are based on aerobic processes.

Oxygen may however, be severed as the terminal electron acceptor in metabolism and oxygen limitation sets in (Yang et al. 2009). One possible scenario is that the pollutant may stimulate the indigenous microbial community, resulting in accelerated aerobic metabolism and a consequent depletion of available molecular oxygen. Replenishment rate of depleted oxygen is usually comparatively slow, and so, anaerobic zones are formed within and close to the contaminated site (Bamforth and Singleton 2005). Under such oxygen-deficient conditions, anaerobic biodegradation may be triggered. Unlike aerobic biodegradation, anaerobic microorganisms utilize other available substrates such as nitrate, sulphate, iron, manganese and carbon dioxide as their electron acceptors to break down hydrocarbons often producing carbon dioxide and methane as the final products (Gan et al. 2009). Alternatively, some anaerobic microorganisms can degrade organic contaminants by fermentation in which case the organic contaminants act as the electron acceptors (Gan et al. 2009; Ukiwe et al. 2013). Another possible scenario is when contamination is high, in which case anaerobic biodegradation may be enforced restricting oxygen diffusion due to organic matter pore saturation or clogging of aggregates (Gan et al. 2009). In cold regions, oxygen supply is a common constraint where oxygen is usually scarce and diffusion can be partly or completely blocked (Yang et al. 2009). There is no air phase in groundwater, and thus the availability of oxygen as an electron acceptor is greatly diminished, limited by the low aqueous solubility of oxygen (estimated to be 12 mg/L at 5 °C). This typically results in anoxic conditions within petroleum-contaminated plumes in groundwater.

As such, anaerobic biodegradation is appealing for the remediation of accidental oil spills and contaminated areas with anoxic conditions such as waterlogged and underground soils, sediments and aquifers (Bamforth and Singleton 2005; Prince 2010; Karigar and Rao 2011). Although anaerobic biodegradation proceeds at a much slower rate, it is an important process that has prospects to clean up anaerobic zones since a large aeration area is not necessary and this may minimize cost (Bamforth and Singleton 2005). BTEX compounds have been degraded under various anaerobic conditions (Krumholz et al. 1996; Leahy and Colwell 1990). BTEX biodegradation in a biofilm system under nitrate-reducing conditions (Arcangeli and Arvin 1994) and biodegradation of toluene in iron-reducing aquifer zones have been reported (Albrechtsen and Christensen 1994).

18.7.4 Moisture

Living cells require liquid water for survival and metabolism (Margesin 2017). Physically, in many different environments such as soil, water acts as an agent of transport by mass flow as well as a medium through which substrates and other reactants diffuse to and from reaction sites (Paul 2014). Microbial motility and spacial proliferation as well as substrate transport are other functions of water in soil (Smiles 1988). Chemically, it acts as a solvent in important biochemical reactions (Paul 2014).

There is a persuasive body of evidence indicating that microorganisms can survive harsh environmental conditions such as sub-optimal temperature provided liquid water is available. Moisture and water activity is more critical for microbial life in terrestrial ecosystems compared to aquatic ecosystems (Leahy and Colwell

1990). Hydrocarbon metabolism in terrestrial environments may be limited by water availability for microbial growth and metabolism because the water activity or potential (a_w) of soils ranges between 0.0 and 0.99 a for most bacteria and above 0.86 a for most actinomycetes and fungi in contrast to aquatic environments, in which water activity is stable at around 0.98 (Leahy and Colwell 1990; Dion and Nautiyal 2007). In water-deprived soils, sometimes, a hydrocarbon-mediated reduction in the water-holding capacity of soils may be induced to provide moisture necessary for microbial metabolism and not inhibit degradation. Dibble and Bartha (1979) illustrated this in a study, in which optimal oil sludge degradation rates in soil were observed at 30–90% water saturation. No inhibition of degradation at the lower values was reported. Soil fungal species have a higher capacity to tolerate water stress compared to prokaryotes (Zumsteg et al. 2013; Romaní et al. 2017). Hyphal growth, which provides cross dried pores and procures water from smaller pores that can hold water longer, is an advantage (Killham 1994; Dion and Nautiyal 2007). Some organisms, for example, lichens, can even survive on water vapour rather than liquid water (Kappen et al. 1995; Esseen et al. 2017). Dry soils are particularly prone to large diurnal temperature fluctuations compared to wet soils because of the high specific heat (Paul 2014). Spatial patterns and high spatial heterogeneity are typical in dry soil ecosystems. The microorganisms in such habitats, therefore, have to adapt to severe thermal contrasts, strong UV and light intensities and inadequate nutrients in addition to negligible precipitation rates (Mykytczuk et al. 2013). Many extreme environments such as polar and alpine habitats, desert regions, etc. experience very dry conditions and low precipitation (Mykytczuk et al. 2013; Goordial et al. 2016). However, some microorganisms are able to adapt and thrive under these low moisture conditions (Margesin and Schinner 2001). Xerotolerant microorganisms may counterbalance low water potential in the environment by accumulating highly soluble small molecules in the cytoplasm (Kempf and Bremer 1998). They accumulate solutes (which may be organic or inorganic molecules)- such as;- amino acids, polyols, carbohydrates, quaternary ammonium compounds which enables them to withstand water and even salt stress (Killham 1994; Kempf and Bremer 1998). These are termed compatible solutes or osmoprotectants, some of which may be constitutively produced and others induced. This results in decreased internal water potential and can influence and modulate specific enzyme activities, but they do not inhibit the overall metabolism capacity of the cells (Dion and Nautiyal 2007). Although energy intensive, osmoregulation is another strategy that enables microorganisms particularly in soils to conserve intracellular enzyme activities under water stress conditions (Dion and Nautiyal 2007). Another strategy against desiccation, which is usually adopted by prokaryotes, is the production of extracellular polysaccharides which retain water (Wright et al. 2005). Formation of microaggregates of cells where elevated water activities are retained may further protect microorganisms from desiccation (Or et al. 2007). Actinomycetes are particularly well osmoregulated, as their cell membranes are selectively permeable, restricting salt ions to cells' exterior while retaining organic solutes within the cells. Like fungi, they can differentiate into dormant cells that are resistant to drying (Dose et al. 2001). Photosynthetic cyanobacteria, which are the primary inhabitants in many dry habitats (Wynn-Williams 2000; Dong and Yu 2007), commonly live a few millimetres below the surface of translucent rocks, such as quartz (Schlesinger et al. 2003), sandstone pebbles (Wynn-Williams 2000), halite (Wierzchos et al. 2006) and gypsum (Dong et al. 2007). These microhabitats support microbial life because they provide adequate supply of CO_2, N_2 and light, which aid photosynthesis and N_2 fixation on the one hand and offer protection from intolerable levels of irradiation, high temperature and arid surface conditions on the other (Cockell and Raven 2004; Dong and Yu 2007). Heterotrophic bacteria are also ubiquitous in desert environments, and their abundance has been linked to mean annual precipitation (Lacap et al. 2011; Maier et al. 2018). In the hyper-arid core region of the Atacama Desert, the heterotrophic groups seem to prefer the soil subsurface (25–30 cm in depth) as opposed to the more hostile surface (Drees et al. 2006; Navarro-González et al. 2003).

In deserts, microbiota have been observed to inhabit pores in sandstones, and some tend to form biological soil crusts (Dion and Nautiyal 2007). In the Ross Desert, an Antarctic cold desert, cryptoendolithic microorganisms grow in the near-surface layer of porous sandstone rocks, where the microclimate is less hostile (Friedmann 1982, 1986). They depend on the unsteady interactions between biological and environmental factors for survival, and alterations that create unfavourable conditions may terminate them (Friedmann and Weed 1987). It has been suggested that tar balls deposited on beaches may represent another situation in which available water limits hydrocarbon biodegradation (Atlas 1977).

On the other extreme, coastal areas are submerged with seawater during tidal and wave movements and only experience transient drought seasons. Soil moisture content is inversely proportional to the degree of aeration. Desert soils are therefore, well aerated most of the time (Godoy-Faúndez et al. 2008). Microbial activities in dry soils may be enhanced by increasing the water content, but this should be done in a controlled manner, to avoid water logging, which can inhibit the growth and metabolism of aerobic species. Many hydrocarbonoclastic microorganisms are aerobic, excessively high moisture levels, therefore, may be a rate-limiting factor in waterlogged areas (Wilkinson et al. 2002).

18.7.5 Nutrients

Many extreme environments are characterized by poor organic and inorganic nutrients (Jiang et al. 2012; Speight and El-Gendy 2018c). Most of the indigenous microorganisms in these environments therefore are usually oligotrophs (adapted to low nutrient supply rates). Cold environments (e.g. cold soils) typically do not support significant amount of plant biomass, organic matter is, therefore, deficient offering less favourable growth conditions for microbes (Speight and El-Gendy 2018b). Overall, nutrient stress influences soil microbiota, selecting for organisms adapted to (intermittent or constant) nutrient stress (Dion and Nautiyal 2007; Torsvik and Øvreås 2008). In ecosystems such as polar and high-elevation alpine soil systems, there is a direct relationship between nutrient levels and moisture content (Dion and Nautiyal 2007). Low nutrient availability is one of the most crucial limitations for microbial physiological and enzymatic processes in desert habitats (Das and Dash 2014). In poor desert soils, microalgae and cyanobacteria, which are major sources of organic materials, are nutrient starved (Dion and Nautiyal 2007). Bacterial survival mechanisms such as the ability for growth at low nutrient concentrations as well as the ability for dormancy to counter starvation have been described (Jannasch 1967; Roszak and Colwell 1987). Another possible survival strategy is a shrinking in cell size via multiple division, thus generating the so-called ultramicrobacteria (Novitsky and Morita 1976, 1977, 1978; Morita 1982). The smaller the bacterial cell, the larger its surface-to-volume ratio, and consequently the greater is its potential for accumulating diluted nutrients from the external environment. Some starving bacteria with a depleted amino acid pool exhibit the so-called stringent response (Neidhardt et al. 1990) which ultimately reduces the protein synthesis rate by inhibiting rRNA synthesis. Other mechanisms for adaptation to low nutrient levels include microbial ability to utilize several substrates as carbon sources simultaneously (Dion and Nautiyal 2007; Eichorst et al. 2007). In areas where fluctuations in nutrient supplies are common, prokaryotes can store nutrients as intracellular polymers (like polysaccharides, poly-β-hydroxybutyrate, polyphosphate). In typical oligotrophic environments, however, particularly cold environments, nutrient supply may be too low to sustain any intracellular storage (Torsvik and Øvreås 2008). There is some research indicating that the organism's affinity for substrates decreases at low temperature due to loss of membrane fluidity that impedes active nutrient transport and the minimum nutrient substrate concentration required for growth increases near the organism's lower temperature limits (Dion and Nautiyal 2007). If liquid water, which is a general necessity for cellular life is present, growth inhibition due to cold temperature conditions may be due to inefficient nutrient uptake, and nutrients invariably become so low to the point where the cell's minimum requirements for sustenance are no longer met (Dion and Nautiyal 2007).

Assuming that proficient microbial degraders are available, unavailability of requisite nutrients may be a rate-limiting factor (Vasudevan and Rajaram 2001). In addition to hydrocarbons, which have been established to serve as carbon sources for some microbial groups, the presence of inorganic nutrients such as nitrogen, phosphorus and potassium is critical because microorganisms require these for incorporation into biomass (Bamforth and Singleton 2005). The supply of these nutrients is however, dependent on certain factors. The nature of the spill or pollution plays a major role; comparison of the biodegradation of hydrocarbons within an oil slick or the biodegradation of soluble hydrocarbons is a typical example (Leahy and Colwell 1990). When considering an oil slick, there is a mass of carbon available for microbial growth within a limited area. In this case, sometimes, diffusion rates are inadequate to provide sufficient nutrients and oxygen to establish optimal C/N and C/P ratios for microbial growth and cellular metabolism (Vasudevan and Rajaram 2001). Toxic effects may also be exerted on microbial consortia by volatile hydrocarbons (Leahy and Colwell 1990). When considering soluble hydrocarbons, nitrogen and phosphorus are probably not limiting since hydrocarbon solubility is so low as to preclude establishment of an unfavourable C/N or C/P ratio (Atlas 1991).

Petroleum hydrocarbons typically contain low concentrations of inorganic nutrients, and hydrocarbon pollution spikes carbon levels at contaminated sites (Sarkar et al. 2005). Available nutrients may become rapidly depleted during microbial metabolism disrupting the C/N or C/P ratio or both, creating unfavourable conditions for microbial growth (Bamforth and Singleton 2005). Contaminated sites are therefore, commonly supplemented with nutrients such as nitrogen and phosphates using oleophilic fertilizers such as paraffinized urea, octylphosphate, ferric octoate, etc. as well as fish bones, animal meal, biosurfactants and other bulking agents to stimulate the in situ microbial community and therefore, enhance biodegradation (Vasudevan and Rajaram 2001; Van Hamme et al. 2003).

The efficacy of this strategy, however, depends on the characteristics of the contaminated site. For instance, the variable and complex composition of soils as well as other factors such as occurrence of nitrogen reserves and the nitrogen-fixing bacteria may influence the efficacy of any nutrient supplementing intervention (Vasudevan and Rajaram 2001). Nutrient amendment to facilitate hydrocarbon degradation should, however, be done cautiously. For instance, supplementing with high nutrient doses in soils with low moisture content could result in increased ionic strength of the liquid, which may inhibit microbial activity. In temperate soils, the (frequent) freeze-thaw cycles may dynamically redistribute the added nutrients affecting their bioavailability (Margesin 2017). In polar soils, it is prudent to add the necessary nutrients in smaller doses over time rather than all at once. Other concerns include the potential toxicity of these treatments if these are leached into receiving water bodies.

18.7.6 Pressure

High pressure is prevalent in habitats such as the deep sea, groundwater, deep sediments or oilfields (Margesin and Schinner 2001). Barophiles (piezophiles) are microorganisms that require high pressure for growth or thrive under pressure conditions higher than atmospheric pressure (Prieur and Marteinsson 1998). Although barophilic (piezophilic) microorganisms have been isolated and described, their ability to sequester hydrocarbons has not been satisfactorily explored (Grossi et al. 2010; Caumette et al. 2015). Pollutants with densities greater than that of marine waters may sink to the deep benthic zone, where the hydrostatic pressure is notably high (Gallego et al. 2018). A combination of high pressure and low temperatures in the deep ocean affects the metabolism of oil-degrading species, thereby inhibiting microbial degradation (Alexander 1999; Prince and Walters 2016).

The effect of hydrostatic pressure on well-known, conventional oil degraders is worth exploring (Grossi et al. 2010). Hydrostatic pressure seems to impair the metabolism of *Alcanivorax* spp., a typical hydrocarbonoclastic microbe that has been identified in many petroleum-impacted environments but was detected in low numbers in the Deepwater Horizon (DWH) oil plume. The low *Alcanivorax* abundance in the DWH deep sea plume and sediment was unrelated to HC concentrations, and its role in bioremediation in this case was considered negligible (Mapelli et al. 2017). Buttressing *Alcanivorax* spp.'s oil-degrading potential and ubiquity in oil-polluted environments, and illustrating the effects of high pressure on its growth and proliferation, *Alcanivorax* was abundantly cultivated under atmospheric pressure from oiled beach sands, oil mousses (collected on surface waters) and plume samples (Kostka et al. 2011; Liu Zhanfei and Liu Jiqing 2013; Gutierrez et al. 2013). Also, hydrostatic pressure of 5 MPa and 10 MPa induced substantive reduction in cell replication and inhibited the growth of *Alcanivorax borkumensis*, *A. dieselolei* and *A. jadensis* on dodecane as sole source of carbon, respectively (Scoma et al. 2016a, b; Scoma and Boon 2016).

18.7.7 pH

It has been postulated that the optimum pH range for hydrocarbon mineralization is neutral (Aislabie et al. 2012). Microorganisms are however, able to withstand suboptimal pH although fungal species are more tolerant of acidic conditions, compared to bacteria (Leahy and Colwell 1990; Al-Daher et al. 1998). Studies have shown the effects of pH on the rate and efficiency of petroleum hydrocarbon biodegradation. Improved gasoline biodegradation (almost double the normal rates) in an acidic (pH 4.5) soil was achieved by adjusting the pH to 7.4 (Verstraete et al. 1976). A significant drop in biodegradation rates was however, observed when the pH was further raised to 8.5. Similarly, pH range 5.0–7.8 was assessed to determine the optimum pH for oily sludge mineralization in soil, and 7.8 was observed to be the optimum (Dibble and Bartha 1979). Lower microbial mineralization rates of octadecane and naphthalene at pH 5.0 compared with pH at 6.5 were observed by Hambrick et al. (1980). Octadecane mineralization rates increased further when the pH was raised from 6.5 to 8.0, although naphthalene mineralization rates did not (Hambrick et al. 1980).

Many times, petroleum-impacted environments are not at the optimal pH for bioremediation (Prince 2010). Soil pH is more variable ranging from 2.5 in mine spoils to 11.0 in alkaline deserts, compared to most aquatic ecosystems which have a more steady pH range (Leahy and Colwell 1990). Further, anthropogenic activities may alter pH and thereby impair biodegradability (Margesin and Schinner 2001). Retired gasworks sites, which are usually replete with demolition waste such as concrete and brick, have been used as case studies. The leaching of these wastes increases the pH of the soil, creating unfavourable conditions for microbial metabolism (Bamforth and Singleton 2005). In addition, the oxidation and leaching of coal spoil creates an acidic environment through the release and oxidation of sulphides. The indigenous microorganisms at these sites might not have the capacity to transform PAHs under acidic or alkaline conditions. The pH at these sites may then be adjusted, by the addition of lime, nutrients or fertilizers to facilitate bioremediation (Wilson and Jones 1993; Alexander 1999; Bamforth and Singleton 2005).

Acidophiles have been isolated and described in the literature (Peeples 2014; Speight and El-Gendy 2018a, b, c, d). Many of these are heterotrophs, which are usually resistant to heavy metals and organic compounds, but have demonstrated remarkable potential to replenish acidic environments contaminated by petroleum hydrocarbons (Bamforth and Singleton 2005). Efficient petroleum biodegradation in aquifers with pH of 4.5–5 has been described (Margesin and Schinner 2001). Also hydrocarbonoclastic microorganisms were found in a tropical, acidic forest soil (pH 4–6), 17 years after an extensive oil spill (Amadi et al. 1996).

Twenty-three heavy-metal-tolerant, acidophilic heterotrophic bacteria, isolated from an acidic mine effluent, metabolized a range of aliphatic hydrocarbons (including 5 mM propane-1-ol, acetone, acetaldehyde, propanaldehyde, dodecanoic acid, hexadecanoic acid, dodecane, hexadecane, 1-chlorohexane) as the sole carbon source at pH 3. Stapleton et al. (1998) reported the biodegradation of aromatic hydrocarbons and PAHs in extremely acidic environments. Three soil samples collected from a long-term coal pile storage basin were investigated; the pH value of areas greatly impacted by runoff from the storage basin was 2. The autochthonous microorganisms mineralized around 50% of the supplied naphthalene and toluene to CO_2 and water within 24 weeks, although only about 10–20% mineralization of phenanthrene and anthracene was achieved. 16sRNA sequence analyses indicated the presence of acidophilic bacteria in the soil samples, but a microbial consortium, including eukaryotes, rather than individual acidophiles was suggested to be involved in biodegradation in this acidic environment (Stapleton et al. 1998).

Although many other industrial capabilities and potentials of alkaliphilic and alkalitolerant microorganisms have been described, there is a paucity of data regarding their use in environmental clean-up (Santini et al. 2016). The bioremediation of phenol at pH 10 by alkaliphilic strains such as *Arthrobacter* sp., *Bacillus cereus*, *Citrobacter freundii*, *Micrococcus agilis* and *Pseudomonas putida* biovar B has however, been described (Kanekar et al. 1998). An alkaliphilic and halophilic bacterium *Nocardioides* sp. (pH 9.5–10 and 10% salinity) isolated from Alkali Lake (Oregon) also demonstrated ability to degrade chlorophenol compounds 2, 4-dichlorophenol, 2,4,5-trichlorophenol and 2,4,6-trichlorophenol as the sole carbon source (Maltseva and Oriel 1997).

18.8 Biosurfactants

Biosurfactants are surface-active, amphiphilic molecules that have hydrophobic and hydrophilic domains, synthesized by microorganisms (Ławniczak et al. 2013). They are structurally diverse and are classified based on microbial origin, mode of action, chemical composition and structure, molecular weight and physicochemical properties (Nguyen et al. 2008; Nievas et al. 2008). They possess remarkable capabilities to interact with a versatile range of hydrocarbons as well as the capacity to lower surface and interfacial tension of liquids and form micelles and microemulsions between two different phases (Ławniczak et al. 2013). They are environmentally friendly, biodegradable and less toxic (compared to their synthetic counterparts) (Karlapudi et al. 2018).

Based on molecular weight, they are classified into low-molecular mass compounds including molecules such as trehalose; lipids, glycolipids, phospholipids, polyol lipids, rhamnolipids and lipopeptides, proteins and surfactins (Smyth et al. 2010). These reduce the surface tension at the air/water interfaces and the interfacial tension at oil/water interfaces. The high molecular weight variants also known as bioemulsifiers (e.g. emulsan, liposan, mannan amphipathic polysaccharides, proteins, lipopolysaccharides, lipoproteins or complex mixtures of lipopeptides, glycolipids, neutral lipids and fatty acids) are amphiphilic and polyphilic polymers that stabilize oil-in-water emulsions (Cameotra and Bollag 2003; Smyth et al. 2010). Although they do not lower the surface tension as effectively as LMW surfactants, they increase the surface area available for bacterial biodegradation (Cameotra and Bollag 2003). Their use as additives to counter the low aqueous solubility of HMW petroleum hydrocarbons and enhance the efficiency of bioremediation has been described (Gan et al. 2009).

Biosurfactants facilitate the transport of hydrophobic contaminants into the aqueous phase through specific interactions resulting in solubilization, thereby increasing their bioavailability, which potentially makes them more susceptible to biodegradation (Maier and Soberón-Chávez 2000). They enhance hydrocarbon biodegradation by two mechanisms (Pacwa-Płociniczak et al. 2011). The first involves increasing substrate availability for microorganisms, while the other involves interaction with the cell surface, which increases the hydrophobicity of the surface, allowing hydrophobic substrates to associate more easily with bacterial cells (Mulligan and Gibbs 2004). By reducing surface and interfacial tensions, biosurfactants increase the surface area of insoluble compounds leading to increased mobility and bioavailability of hydrocarbons (Bordoloi and Konwar, 2009). For LMW biosurfactants, above the critical micelle concentration (CMC), a significant fraction of the hydrophobic contaminant partitions in the surfactant micelle cores. In some cases, this results in a general increase in the bioavailability of contaminants for degrading microbiota. Microorganisms such as *Candida bombicola*, *C. apicola*, *Rhodotorula bogoriensis*, *Pseudozyma* yeasts, *Pseudozyma aphidis*, *Pseudozyma antarctica*, *Pseudozyma rugulosa*, *Alcanivorax borkumensis*, *Mycobacterium* spp., *Nocardia* spp., *Corynebacterium* spp., *Bacillus subtilis*, *Pseudomonas aeruginosa* and *Torulopsis bombicola* have been reported to produce surfactants such as trehalolipids, surfactin, glucolipid, rhamnolipid and sophorolipid (Maier and Soberón-Chávez 2000; Kuyukina et al. 2005; Chevron Cottin and Merlin 2007; Konishi et al. 2007; Kadri et al. 2018).

The capability of biosurfactants and biosurfactant-producing bacterial strains to enhance availability of petroleum hydrocarbons and biodegradation rates has been reported by many authors (Rapp et al. 1979; Rahman et al. 2003; Inakollu et al. 2004; Obayori et al. 2009; Reddy et al. 2010). Hydrocarbonoclastic microorganisms have been demonstrated to synthesize and release biosurfactants which greatly enhance their effectiveness in uptake and sequestration of hydrocarbons (Broderick and Cooney 1982; Singer and Finnerty 1984). Enhanced solubilization and a concomitant improved mineralization of phenanthrene, pyrene and fluorene by lipopeptide and protein-starch-lipid produced by two *P. aeruginosa* strains have been described (Bordoloi and Konwar 2009). The production and emulsification activities of biosurfactants are influenced by environmental factors such as salinity, pH and temperature, but they have been described to be highly reactive and active at extreme temperatures, pH and salinity (Das et al. 2008; Pacwa-Płociniczak et al. 2011). Hydrocarbon-degrading marine bacteria *Rhodococcus fascians* isolated from the Antarctic produced bioemulsifiers when cultured with *n*-alkanes as sole carbon source (Yakimov et al. 1999). The *R. fascians* strains utilized hexadecane and biphenyl as sole carbon sources at temperatures ranging from 4 to 35 °C, with optimum degradation achieved at 15–20 °C (Yakimov et al. 1999; Margesin and Schinner 2001). Biosurfactant-producing organisms from Tunisian oilfields have also been characterized (Mnif et al. 2011). Psychrophilic strains with high oil-oxidizing and bioemulsifying activities were also described by Chugunov et al. (2000).

A variety of applications for biosurfactants has been described. The molecules could be added externally (influent, spraying or injection) or could be produced on site, which seems especially promising in the case of in situ treatment (Ławniczak et al. 2013). In the latter case, biosurfactants may be produced by bioaugmentation, using metabolically competent strains since autochthonous microorganisms rarely exhibit satisfactory efficiency (Ławniczak et al. 2013). The roles of biosurfactants in biodegradation have been characterized mostly by observing the effects of fractionated preparations (Patowary et al. 2017). However, the successful application of biosurfactants in bioremediation of petroleum pollutants will require precise targeting to the physicochemical conditions of the contaminated areas (Van Hamme et al. 2003). Although the potential of biosurfactants in facilitating bioremediation has been extensively documented, the dynamics of use to replenish polluted extreme habitats are yet to be fully explored.

18.9 Bioremediation of Petroleum Hydrocarbons in Cold Regions

In cold regions such as the Arctic, Alpine, Antarctic, polar and deepwater regions, petroleum hydrocarbon pollution is an important environmental problem (Braddock et al. 1997; Aislabie et al. 1998; Delille et al. 1998; Margesin 2000; Delille and Delille 2000; Lin et al. 2009; Yang et al. 2014). In the cold areas of some countries such as Canada, Russia, the United States (Alaska) and China (Qinghai-Tibet Plateau), petroleum hydrocarbon contamination has been extensively documented (Collins et al. 1993; Margesin and Schinner 1999; Chuvilin et al. 2000; Yang et al. 2009). Resource exploration, transportation, storage and handling of petroleum products with potential for spillage pose significant environmental risks for cold marine and terrestrial ecosystems (Filler et al. 2008). In the Arctic, for example, crude oil spills from ruptured pipelines represent one of the most significant sources of terrestrial petroleum pollution, followed by shoreline spills from tankers or resupply vessels (Engelhardt 1994). Refined fuel spills are also quite common (Margesin 2017). These are usually caused by infrastructural mishaps, human error during fuel transfer, sabotage or vandalism or natural hazards (Filler et al. 2008). Local physicochemical, geological and biological conditions influence the success of remediation strategies in these regions (Margesin 2017). The unique environmental variables affect the efficiency and rate of bioremediation. Some of these include occurrence of permafrost, water lying above the permafrost, physiology and biochemistry of psychrophiles/psychrotolerant microbes, extreme fluctuations in daily solar radiation levels year round, cold ground and air temperatures as well as annual freezing and thawing of surface layers (Filler et al. 2008).

Petroleum HC contamination in cold regions has potential to be more catastrophic due to the remote locations, limited infrastructure, cold temperature and other environmental constraints related to temperature such as inadequate moisture, low nutrient availability, incidence of competent hydrocarbon-degrading consortia, etc. which pose formidable challenges for remediation (Van Stempvoort and Biggar 2008; Margesin 2017). Hydrocarbon pollutants can persist for several years in these ecosystems because natural attenuation is significantly slower compared to regions with moderate climatic conditions. Bioremediation in cold regions, therefore, may prove to be problematic. For instance, attempts to degrade oil contamination in Arctic marine ice and frozen tundra soil yielded only very limited success (Atlas 1979). Adverse winter temperatures limited the biodegradation of PAHs in estuarine sediment (Shiaris 1989) and of a variety of hydrocarbons in fresh water lakes (Cooney et al. 1985). Gunkel (1967) reported very low hydrocarbon utilization rates at low temperatures. Improved motor oil oxidation rates at 20 °C compared to 5 °C were described by Ludzack and Kinkead (1956), and a similar finding by ZoBell (1969) showed that hydrocarbon degradation was over an order of magnitude faster at 25 °C than at 5 °C. Also, significantly long persistence times for oil in tundra soils were observed by Sexstone and Atlas (1978) and Sexstone et al. (1978). Apparently, hydrocarbon degradation ceases during winter when tundra soils are frozen. In spite of these, however, successful biodegradation of oil in habitats with low temperature has been reported (ZoBell 1973; Cundell and Traxler 1973; Eriksson et al. 2001; Gibb et al. 2001; Hazen et al. 2010; Garneau et al. 2016). Furthermore, it is quite apparent that the microorganisms adapt to the contamination, indicated by the higher microbial activity of certain species post contamination (Whyte et al. 1999). Survival of adapted microorganisms usually depends on their hydration state, their compatible solute content and their ability to switch metabolism to cryoprotectant synthesis (Dion and Nautiyal 2007; Liang et al. 2013).

Cold-adapted autochthonous microbial assemblages capable of rapidly degrading crude oil constituents at subzero or near-zero temperature profiles have been isolated and characterized (Yakimov et al. 2004). Growth at low temperatures requires significant membrane alterations to maintain the fluidity required for nutrient transport across the membrane. Low temperature modifications involve less saturated and less branched membrane fatty acids. Below the minimum growth temperature, the membrane becomes solid, and transmembrane transportation is halted (Dion and Nautiyal 2007). Mechanisms and appendages that facilitate life at these cold temperatures have been investigated (Médigue et al. 2005). Microorganisms may accumulate antifreeze compounds (high salt concentrations, hydrocarbons or amino acids) in the cytoplasm (Margesin et al. 2007; Fuchs et al. 2013; Moreno and Rojo 2014). Bacteria and Archaea have similar adaptive mechanisms, which involve altered membrane composition (cold-adapted lipids) as well as cold-active proteins involved in fundamental cell functions (such as protein synthesis) (Cavicchioli et al. 2000). For psychrophiles, specific cold adaptation implies such drastic changes in cell biochemical composition and makes them unsuited for life outside cold temperatures (Dion and Nautiyal 2007). For instance, the enzymes and ribosomes of cold-adapted microbes become unstable at temperatures 1–2 °C above their 'optimum' temperatures. Accordingly, the psychrophiles have optimum temperatures at or below 15 °C and maximum temperatures below 20 °C. These psychrotrophic organisms can also grow at temperatures close to or even below 0 °C, but their optimum temperature is above 15 °C, and their maximum temperature limit can be as high as 30–40 °C. Cryopegs, which are characteristic features of permafrost regions, are thin films of liquid water, present in permafrost or in permafrost brine lenses. They are generated from layers of unfrozen ground that are perennially cryotic (forming part of the permafrost), but in which freezing is prevented by freeze-point depression due to high concentrations of dissolved substances in the pore water. They may serve as an ecological niche where enzymatically and metabolically active microbes subsist at below freezing temperature (Gilichinsky et al. 2003). They support microbial growth at temperatures as low as −10 °C and metabolic activity at −20 °C and even lower (Bakermans et al. 2002).

The feasibility of bioremediating hydrocarbon-contaminated ecosystems in cold regions has been demonstrated (Margesin and Schinner 2001; Mohn et al. 2001; Yang et al. 2009). A diverse group of bacterial and fungal species capable of not only proliferating under cold conditions but metabolizing hydrocarbons have been identified by numerous studies (Vasco et al. 2011; Kosek et al. 2016). In soil, a broad range of crude oil aliphatics (C_{10}–C_{21}), branched alkanes and a substituted cyclohexane was metabolized by a psychrotrophic *Rhodococcus* sp. at 5 °C (Whyte et al. 1998). Short-chain alkanes (C_{10}–C_{16}) were significantly mineralized better (by a factor of 2–3), compared to long-chain alkanes (C_{28} and C_{32}) at 0 and 5 °C. Long-chain alkanes are less bioavailable at low temperature; factors such as the tendency to form crystals at 0 °C seem to contribute to this, as this increases their persistence and ultimately affects in situ bioremediation in cold climates. Rike et al. (2003) carried out in situ biodegradation of petroleum hydrocarbons in frozen Arctic soil. The study concluded that 0 °C is not the ultimate limit for in situ cold-adapted microbial-mediated biodegradation of petroleum hydrocarbons and that biodegradation can proceed at subzero temperatures during winter in the investigated site (Margesin and Schinner 2001). In Antarctic soils, cold-tolerant species such as *Pseudomonas* spp. and *Sphingomonas* spp. isolated from the soils degraded hydrocarbons such as naphthalene, phenanthrene, fluorene, hexadecane as well as BTEX as sole carbon and energy source (Aislabie et al. 1998, 2000). Using phenanthrene as a model compound, 53 PAH-metabolizing bacteria were isolated from diesel-contaminated Antarctic soil samples, three of which exhibited a high phenanthrene-degrading capacity (Gran-Scheuch et al. 2017). In Northern soils, microbial populations degraded hydrocarbons at ambient temperatures prevalent during the warmer seasons (Jobson et al. 1972; Westlake et al. 1978).

The technological feasibility of in situ bioremediation of hydrocarbons in cold groundwater systems has been demonstrated by some studies. Bradley and Chapelle (1995) described rapid aerobic toluene mineralization in sediments from a cold (mean groundwater temperature 5 °C) petroleum-contaminated aquifer in Alaska.

18.9.1 Fate of Hydrocarbon Pollutants in Cold Regions

Determining an effective range of suitable remedial strategies for cold regions is a major challenge for environmental managers, engineers and scientists. The degree of success in mitigating the environmental and economic impacts of petroleum pollution in cold regions depends on a variety of factors. The treatment of petroleum hydrocarbon pollution (e.g. oil spill) in cold regions usually involves containment and removal as the first line of action (Kadri et al. 2018). Some possible options include excavation and inland incineration. Excavating and relocating pollutants for off-site treatment are in many cases not viable, because the costs and environmental impacts of bulk extraction may equal or exceed damage caused by the initial pollution (Filler et al. 2008). Similarly, in-ground incineration will not effectively ameliorate oil spill pollution but would rather cause downward migration of pollutants and permafrost degradation through heating. Bioremediation, which is more practical and sustainable, is usually executed after the containment and removal (Yang et al. 2009). Seasonal variations in the rates of hydrocarbon biodegradation under cold temperatures have been observed. In cold regions, hydrocarbonoclastic microorganisms are more abundant during winter than other seasons (Atlas and Bartha 1973; Atlas 1981). For example, higher numbers of hydrocarbon utilizers capable of growth at 5 °C were present in Raritan Bay, N.J., during winter compared to other seasons. Also, rates of hydrocarbon mineralization measured at 5 °C were significantly higher in water samples collected in winter than in summer (Atlas 1981). During summertime, in Arctic surface waters, different structural classes of hydrocarbons were metabolized at similar rates (Horowitz and Atlas 1977). Slower but more extensive biodegradation of petroleum hydrocarbons under cold temperature conditions (0 °C) than at higher temperatures has been demonstrated using a model incubated with estuarine water collected during winter (Walker and Colwell 1974). The better growth observed was attributed to decreased toxicity of hydrocarbons at lower temperatures. Ward and Brock (1976) reported a relationship between seasonal changes in temperature and oxidation of hexadecane with optimum degradation rates at 20–25 °C in the summer. Similarly, crude oil mineralization in soil samples from Louisiana salt marshes varied depending on the season (Jackson and Pardue 1997). During the transition period of spring and fall, the degree of success may be extensively modified, depending on whether or not the contaminated sites are in close proximity to pollution sources and the occurrence of surface ice or heavy runoff. The characteristics (e.g. solubility and viscosity) of the spilled oil also vary seasonally, and this affects rate and efficiency of biodegradation. Therefore, bioremediation might be needed in certain seasons and not in others. Containment strategy used also depends on the season. Summertime oil spill requires rapid (usually within hours) intervention. In this case, physical removal techniques such as the deployment of a surrounding boom, then vacuum pumping and subsequently, mopping up as much oil as possible using sheets of absorbent materials may be used (Leahy and Colwell 1990).

The influence of co-metabolism makes it difficult to ascertain the direct influence of temperature on bioremediation rates in cold regions. Greater degradation of Metula crude oil at 3 °C than at 22 °C with mixed microbial cultures in beach sand samples was described (Colwell et al. 1978). When 0.1% oil was added, 48% of the added hydrocarbons were degraded at an incubation temperature of 3 °C, compared to only 21% degraded at 22 °C with cultures adapted at the same temperature profiles as the incubation temperature. Under in situ conditions, oil degradation proceeded slowly, but in this study, it was apparent that temperature was not the limiting factor for petroleum degradation in the Antarctic marine ecosystem affected by the Metula spill (Colwell et al. 1978).

Another study assessed crude oil degradation in Arctic marine ice, water and sediment ecosystems. Petroleum hydrocarbons were degraded slowly. Ice immensely inhibited light hydrocarbon losses, and biodegradation of oil on the surface of ice or under sea ice was negligible. It was concluded that petroleum hydrocarbons would remain in cold Arctic ecosystems for protracted periods after oil contamination incidents, although, in these studies, temperature was not specifically elucidated as a major factor limiting hydrocarbon bioremediation except as it related to the occurrence of ice (Atlas and Raymond 1977; Atlas et al. 1978).

18.9.2 Biodegradation of petroleum hydrocarbons in Hot Regions

Thermophilic organisms normally do not thrive at temperatures below 50 °C, whereas the thermotrophs have a lower temperature limit (20–30 °C). At their upper temperature limit, cells become unstable, and irreversible denaturation of proteins and nucleic acids occurs; therefore molecules lose their ability to perform biochemical functions (Price and Sowers 2004; Dion and Nautiyal 2007).

Physiologically and metabolically diverse assortment of thermophilic and hyperthermophilic microorganisms have been identified and characterized from high-temperature, petroleum-contaminated environments (Foght and McFarlane 1999; Orphan et al. 2000; Blanchet et al. 2001). These include sulphate reducers, sulfidogens, fermentative bacteria, manganese and iron reducers, methanogens and acetogens (Davey et al. 1992; Stetter et al. 1993; L'Haridon et al. 1995; Tardy-Jacquenod et al. 1996; Grassia et al. 1996; Greene et al. 1997; Orphan et al. 2000; Magot et al. 2000). Hyperthermophilic Archaea and Bacteria with optimal growth temperatures between 80 °C and 110 °C have been isolated from hot habitats like geothermal and hydrothermal environments. Thermophiles have been isolated from natural thermal soils such as decomposing litter, volcanic, geothermal and tropical desert soils and from manmade thermal soils such as compost piles and coal refuse piles (Botero et al. 2004). For oil-polluted desert soils, for example, indigenous hydrocarbonoclastic thermophiles such as *Bacillus thermoleovorans*, *Geobacillus thermoleovorans* and *B. stearothermophilus* as well as members of *Anaerolineae*, *Thermotogae*, *Gemmatimonadetes*, *Deferribacteres*, *Spirochaetes* and *Thermoleophilica* have been utilized to restore contaminated hot zones such as in the arid regions (Abed et al. 2006). These microbes were reported to significantly accelerate the rate of in situ bioremediation at these sites. Zeikus et al. (1980) demonstrated microbial methanogenesis at temperatures near 70 °C but below 80 °C in thermal waters, muds and decomposing algal-bacterial mats associated with volcanic activity in Yellowstone National Park. At elevated temperature profiles, bioavailability of petroleum hydrocarbon compounds are significantly improved (Camenzuli and Freidman 2015). High temperatures also reduce viscosity and improve diffusion coefficients, thereby improving mass transfer rate to microbial cells. Also, volatile HC fractions usually evaporate rapidly, leaving more hydrophobic HMW constituents to contend with. This could, however, complicate bioremediation efforts as a tar layer may likely form, which then settles over large areas of coast. This tar layer is highly resistant to biodegradation, and bioremediation in such cases becomes irrelevant. Other remediation strategies like the mechanical removal of tar layers may be explored in such cases (Abed et al. 2006).

Very hot ecosystems such as desert soils are poor in organic matter and water and are usually subjected to excessively high temperature in summer, chilly temperature in winter and extensive light. In spite of these extreme characteristics, desert soils usually accommodate microorganisms including members of actinomycetes, cyanobacteria and other bacteria, fungi, protozoa and phototrophic microalgae. Many of these microbes have the capacity to cope with stress and possess adaptive mechanisms for survival and proliferation. A strain closely related to *Geobacillus pallidus* isolated from a tyrosol-degrading enrichment developed from production water from a high-temperature oilfield in Tunisia utilized crude oil and diesel as carbon sources in the presence of 0–12% NaCl (Chamkha et al. 2008).

Microbes adapted to high temperatures have mechanisms to protect their proteins and nucleic acids from denaturation (Dion and Nautiyal 2007). These strategies involve alterations to the membrane composition and functioning which results in decreased membrane fluidity and as a consequence improved thermostability (Dion and Nautiyal 2007). Biomolecules produced are thermostable, with the capacity to remain biochemically active at temperatures that will otherwise inactivate proteins, lipids and nucleic acids in mesophiles (Rothschild and Mancinelli 2001; Dion and Nautiyal 2007). Some proteins become stable due to alterations in amino acid residues, which confer higher hydrophobicity on them, thereby increasing the stability of subunit interactions (Singleton and Amelunxen 1973; Dion and Nautiyal 2007). The nucleic acids are also thermostabilized, for instance, because of the interactions with histone-like proteins. At high temperature, the membrane fatty acids acquire longer chains, becoming more saturated and branched (Dion and Nautiyal 2007).

18.10 Bioaugmentation

Bioaugmentation involves the addition of specifically formulated microorganisms or an inoculum of microorganisms with known pollutant transformation abilities to a contaminated site to reinforce natural biological processes (Tyagi et al. 2011; Sharma 2012). The development and monitoring of an ideal growth environment in which these selected strains can thrive and function form an integral part of this approach. This intervention is based on the premise that the metabolic capacities of the indigenous microbial community existing in the contaminated site will be enhanced by an exogenous genetic diversity, thus leading to a wider repertoire of productive biodegradation reactions (Leung 2004; Cameotra and Bollag 2003). However, certain limitations to bioaugmentation have been identified. One of the most prominent includes the poor competition/survival of added strains commonly because autochthonous microbial community tends to stifle exotic strains (Maila and Cloete 2004). Selective metabolism of compounds, the tendency for microbes to use up readily degradable substrates (hydrocarbon fractions), probably due to low concentrations and no/poor biodegradability potential of targeted compounds, is another important limitation (Maila and Cloete 2004). Some approaches are available to optimize bioaugmentation potential. The most commonly adapted options for bioaugmentation include the addition of a preadapted pure bacterial strain (or consortium), introduction of genetically engineered microorganisms and the incorporation ('seeding') of biodegradation relevant genes from the augmented strains into a vector to be transferred by conjugation into the autochthonous microbial population (El Fantroussi and Agathos 2005; Tyagi et al. 2011). It is recommended that bioaugmentation be conducted in sites with no indigenous hydrocarbonoclastic microbiota, such as sites contaminated by HMW polyaromatic hydrocarbons (Maila and Cloete 2004).

18.11 Biostimulation

Many microorganisms possess intrinsic capacity to degrade or transform various toxic compounds, but these natural transformation processes are relatively slow (Maier and Gentry 2015). This may be due to factors such as insufficient electron acceptors, low activity of functional microorganisms and inefficient electron transfer, all of which affect the efficiency of bioremediation (Li et al. 2018). In order to achieve desired treatment results, environmental conditions, suitable for microbial growth and activity, must be created (Karigar and Rao 2011).

Biostimulation is a technique developed to achieve optimum conditions for microbial growth within contaminated sites (Nwinyi and Olawore 2017). It also involves stimulating the viable microbial population by adjusting water, air and nutrient supply (Wu et al. 2016; Brown et al. 2017). It involves the introduction of additional nutrients (organic or inorganic), bulking agents such as woodchips, compost and electron donors or acceptors to a contaminated site (Namkoong et al. 2002; Scow and Hicks 2005). Some recent biostimulation approaches include the use of microbial electroremediation cells (Li et al. 2018).

18.12 Bioavailability

Bioavailability, referred to as the bioaccessible fraction by some reports, is the percentage of pollutant that microorganisms can readily access and biodegrade or biotransform (Maier 2000; Ortega-Calvo et al. 2013). It is important because it directly influences the efficiency of bioremediation (Ławniczak et al. 2013; Olaniran et al. 2013). According to experts, poor bioavailability limits the full exploitation of in situ bioremediation protocols (Gogoi et al. 2003; Bamforth and Singleton 2005; Harms et al. 2011). The bioavailability of petroleum hydrocarbons is related to the chemistry of the compounds; molecular structure and weight influence bioavailability. The diffusion rate of the hydrocarbons (in soil or sediment) into microbial cells is influenced by chemical activity, and this will influence the bioaccessible fraction (Ortega-Calvo et al. 2013). Polycyclic aromatic hydrocarbons, for instance, are known to partition into sorbents and NAPLs and also tend to adsorb unto organic particulates, which means the chemical activity gradient expression will be weak, which will affect their uptake and transformation by microorganisms (Ortega-Calvo et al. 2013).

Induction of catabolic gene systems used by microorganisms for biodegradation is a high energy expenditure. The presence and concentrations of contaminants significantly impact the metabolic status and activity of microbial cells. Low contaminant levels mean that these genes will not be induced (Maier 2000). Varying bioavailability of contaminants (in terrestrial environments) may result in either of three scenarios.

The first possibility is that biodegradation will not be prompted because the amount of bioavailable contaminant is inadequate and energy expenditure by microbes is not justified (Maier 2000). In the second case, at low bioavailable concentrations, microorganisms may biodegrade contaminants but in a resting or maintenance state rather than an active, growing state (Maier 2000). In this case, biodegradation will indeed occur, but at a limited rate because the microorganisms are not proliferating. The third possible scenario is ample contaminant levels are available, and biodegradation will proceed at optimal rates (Maier 2000). Over time, microorganisms have evolved strategies to counter poor bioavailability (Dua et al. 2002). One of these strategies is the development of increased cell affinity for hydrophobic surfaces, in the case of hydrocarbons with poor aqueous solubility, this enables the degrading species to attach to the hydrophobic substrate and absorb it directly (Maier 2000). The other is the synthesis of surface-active agents or biosurfactants (already explored above). In addition to improving the solubilization of the compounds, dispersal promotion of microorganisms throughout the polluted matrix can also improve bioavailability (Ortega-Calvo et al. 2013).

18.13 Conclusions

Petroleum hydrocarbons are ubiquitous environmental pollutants, which are introduced into the environment accidentally, due to oversight or deliberately during resource exploration, processing, transport and storage. Other anthropogenic activities such as gasification of fossil fuels and other processes involving the incomplete combustion of organic substances also release petroleum hydrocarbons into the environment. In regions characterized by extreme environmental and climatic conditions, petroleum hydrocarbon contamination represents a significant environmental challenge. Petroleum microbiology is influenced by environmental variables, and unfavourable environmental conditions affect the nature of petroleum pollutants, the extent and efficacy of non-biological removal and microbial metabolic capacities. Microbial growth and degradation abilities and, in fact, overall rates of chemical and enzymatic reactions are strongly influenced by suboptimal environmental conditions and, therefore, determine the success of natural attenuation or bioremediation efforts. Many petroleum compounds are hydrophobic, stable and persistent. They are also potential or proven toxicants to the environment, human health and other life forms. The need for clean-up of contaminated sites is widely acknowledged and has been attempted on varying scales. Output of laboratory and field remediation applications abound in the literature. Numerous conventional remediation schemes/approaches have been in use for quite some time, but bioremediation has proven to be effective and eco-friendly and is publicly accepted. Bioremediation strategies and protocols have been designed, optimized and adopted to replenish petroleum-contaminated terrestrial and aquatic habitats, yielding considerable success. Although studies regarding bioremediation in microaerobic, anoxic, anaerobic, hypersaline and other extreme habitats are fewer compared to those on bioremediation in ‘normal’ environments, there are studies that have described the feasibility of bioremediation in extreme environments. Microbial consortia and associations as well as microbial responses and adaptations to environmental stress conditions have been and continue to be investigated, enabling us to understand how extreme polluted environments can be restored. Petroleum hydrocarbon bioremediation potential under extreme conditions and relevant studies have been examined in this chapter. Hydrocarbonoclastic extremophiles, their adaptive strategies/responses and oil utilizing capacities have been described by several studies. Some important dynamics, constraints and certain mechanisms of tolerance have been discussed herein. Considering available studies, microbial treatment of extreme petroleum-impacted habitats seems indeed plausible. It is important to further explore extremophiles, identify and characterize those that have oil utilizing potential and optimize bioremediation protocols for their use. More importantly, however, prevention of hydrocarbon pollution in the first instance is critical and should be the priority of all relevant players and stakeholders.

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