Oil reservoirs, an exceptional habitat for microorganisms

Mark Pannekens¹, Lisa Kroll¹, Hubert Müller, Fatou Tall Mbow, Rainer U. Meckenstock*¹

University of Duisburg-Essen, Biofilm Centre, Universitätsstr. 5, 41451, Essen, Germany

Keywords: Oil reservoir Microbial ecology Biodegradation Oil-water transition zone Biofilm Virus

ABSTRACT

Microorganisms are present in oil reservoirs around the world where they degrade oil and lead to changes in oil quality. Unfortunately, our knowledge about processes in deep oil reservoirs is limited due to the lack of undisturbed samples. In this review, we discuss the distribution of microorganisms at the oil-water transition zone as well as in water saturated parts of the oil leg and their possible physiological adaptations to abiotic and biotic ecological factors such as temperature, salinity and viruses. We show the importance of studying the water phase within the oil, because small water inclusions and pockets within the oil leg provide an exceptional habitat for microorganisms within a natural oil reservoir and concurrently enlarge the zone of oil biodegradation. Environmental factors such as temperature and salinity control oil biodegradation. Temperature determines the type of microorganisms which are able to inhabit the reservoir. Proteobacteria and Euryarchaeota, are ubiquitous in oil reservoirs over all temperature ranges, whereas some others are tied to specific temperatures. It is proposed that biofilm formation is the dominant type of microorganisms, enhancing nutrient uptake, syntrophic interactions and protection against environmental stress. Literature shows that viruses are abundant in oil reservoirs and the possible impact on microbial community composition due to control of microbial activity and function is discussed.

Introduction

Oil reservoirs are extreme environments for microbial life [1] characterized by high toxicity, hydrophobicity and low water activity, as well as high temperature, salinity, and pressure [2]. Nevertheless, oil reservoirs offer a broad range of niches for a multitude of bacteria and archaea, such as sulfate-, nitrate-, and iron-reducers, fermenters, acetogens, and methanogens [1,3]. The microbial degradation of oil results in a higher fraction of bitumen and eventually leads to the deterioration of the world’s oil resources. Since oil is still one of the most important resources for industry and energy [4], it is crucial to gain insights into the microbiology of oil reservoirs. Over the past decades, numerous reviews on oil microbiology have investigated the extent of biodegradation, the effect of microbes on oil quality, oil production methods and enhanced oil recovery (EOR) [3,5–8], as well as their taxonomical and functional composition and the impact of environmental factors on microbes [3,7,9,10]. However, due to the lack of undisturbed samples, our knowledge of microbial ecology in oil reservoirs is still limited [11].

Distribution of microbes within oil reservoirs

Oil reservoirs consist of different phases where microorganisms can thrive, such as crude oil, formation water and solid surfaces from rock and organic materials [12]. To understand the oil-water distribution patterns of microbes, it is important to conceptualize the oil habitat. In general, microbial degradation of oil is limited by the availability of electron acceptors because, due to thermodynamic constraints, hydrocarbons cannot be fermented without a hydrogen and acetate scavenging process. However, microbes can only conserve energy if they have direct contact to both electron donors from the oil phase and electron acceptors from the water phase [13,14]. This situation is found at the oil-water transition zone (OWTZ) beneath the oil leg, which is a hotspot of microbial growth and oil degradation [5,15] (Fig. 1). Here, the oil phase provides electron donors and the water phase provides the habitat for the microorganisms. Consequently, the rate of oil biodegradation depends strongly on the size of the surface of the oil-water interface.

In deep oil reservoirs, dissolved electron acceptors oxygen and nitrate are naturally absent unless anthropogenically added via injected

Abbreviations: OWTZ, oil-water transition zone; EPS, extracellular polymeric substances; PAH, polycyclic aromatic hydrocarbons; EOR, enhanced oil recovery; OTUs, operational taxonomic units; SRB, sulfate-reducing bacteria

*Corresponding author at: University of Duisburg-Essen, Biofilm Centre, Universitätsstr. 5, 41451, Essen, Germany.

E-mail address: rainer.meckenstock@uni-due.de (R.U. Meckenstock).

1These authors are contributed equally to this work and are regarded as joint first authors.

https://doi.org/10.1016/j.nbt.2018.11.006

Available online 28 November 2018

1871-6784/ © 2018 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/BY-NC-ND/4.0/).
fluids [8]. Several studies detected iron-, manganese-, or nitrate-reducing bacteria such as *Shewanella putrefaciens* or *Deferribacter thermophilus* in fluids of oil reservoirs [16–20]. However, solid iron(III) and manganese (IV) oxides typically are not available as electron acceptors for microbial oil degradation because they have been reduced over the millions of years and are not replenished. Therefore, the most prevalent processes are fermentation, methanogenesis and sulfate reduction, if there is a source of sulfate [8,21,22].

It has been a paradigm for the last decades that biodegradation mostly takes place directly near the OWTZ. However, studies have shown an increasing saturated hydrocarbon content over approximately 100–130 m away from the OWTZ due to circulation and diffusion [5]. Nevertheless, there is always a certain amount of water also present in the oil leg either as water-saturated areas in the pore space of the rock or as a thin water film covering the rock surface in water wet reservoirs. Thus, different oil reservoirs vary in water content as well as in their oil composition [5,7,23,24]. Interestingly, oil samples with high water content of around 40–60% harbor a 2.6-fold higher bacterial richness compared to low water content oils with 1–5% [25] indicating that the amount of water present in the oil leg plays an important role as a habitat for the microorganisms.

In fact, stratified water pockets and pore spaces were discovered in the natural asphalts from the La Brea Tar Pits in Los Angeles, CA [26], and small water inclusions were discovered in the oil phase of the Pitch Lake in Trinidad and Tobago, the world largest natural tar lake [27]. The 1–3 μl water droplets from Trinidad and Tobago were densely populated with complex microbial communities and actively degrading the oil. The high salinity and water-stable isotope measurements indicated that the water droplets originated from deep subsurface formation water, most likely directly form the oil reservoir feeding the natural oil seep through a geological fracture [27]. Taking the water droplets as a proxy for subsurface processes, it is very likely that significant microbial populations can thrive within water-filled rock pores away from the OWTZ. Consequently, microbial degradation potential in the reservoir should correlate with the water content of the different phases, building a gradient of degradation activity starting from the OWTZ at the bottom and decreasing to the top of the reservoir (Fig. 1). In fact, such patterns of biodegraded oil can be found in reservoirs although they have been interpreted as diffusion gradients of alkanes from the non-degraded oil at the top of the reservoirs towards the depletion hot spot at the OWTZ [11]. Nevertheless, the findings from Tar Pits in Los Angeles and of the dispersed water droplets in the natural oil seep in Trinidad indicate that microbes reside in water pockets within the oil phase or even in the water film around sand grains [26,27]. This concept enlarges the overall oil-water interface and should be considered as having a large impact on the degradation process. Microbial oil biodegradation can consequently occur not only at the OWTZ, but also within the oil leg (Fig. 1).

Upon production, oil is pumped to the surface as an artificial mixture of water, oil and gas. One has to be aware that this mixture does not necessarily contain the true composition of the microbial communities in the subsurface. Most of the microbes that thrive either at the OWTZ or in the water-filled compartments in the oil leg will thrive attached to the rock matrix rather than planktonic in the water phase and will not appear in oil or produced water. Furthermore, cells not attached to the rock are probably present in dense biofilms at the oil-

![Fig. 1. Schematic scheme of a deep subsurface oil reservoir (oil leg) with underlying brine water (water leg). Most of the biological oil degradation takes place at the oil-water transition zone (OWTZ) and in dispersed water droplets nearby. Microorganisms live attached to rock particles in a thin water film or in dispersed water droplets amidst the oil phase.](image-url)
Thus, the two phases, water and oil, should be analyzed to understand the true community composition. The oil phase contains another part of the microbial communities, most likely containing attached microbes found at the alkane-water interface of n-alkanes (C8–C28) and n-alcohols (C8, C12 and C16) [45,47,53]. Some enrichment cultures were able to build biofilms on the surface of phenanthrene and other PAHs to overcome the mass transfer limitations during the degradation [44,46]. Biofilm formation also depends on the solubility of the PAHs; lower solubility results in more attached cells and biofilm formation to overcome the mass transfer limitations [46]. Due to these advantages of biofilms in toxic and extreme environments, we propose that biofilm formation is also the predominant form of life in oil reservoirs.

**Life in extreme environments – oil as an exceptional habitat**

**Biofilms as a physiological adaptation to life in oil?**

Microbial life in oil reservoirs faces severe conditions with multiple stressors such as toxicity of the oil and low water activity. In addition, planktonic microorganisms often do not have access to both electron donor and electron acceptor as a prerequisite for microbial energy metabolism. Thus, the water phase itself contains only a minor portion of the microbial communities, most likely containing attached microbes and those present in small water droplets dispersed in the oil [9,27]. Thus, at least the two phases, water and oil, should be analyzed to obtain a better picture of the true microbial community composition.

**Metabolic functions and interactions of microorganisms in oil reservoirs**

In the absence of the most favorable electron acceptors oxygen and nitrate, sulfate reduction and syntrophic methanogenesis are the dominant processes in oil biodegradation [3]. If sulfate is present at concentrations higher than 50 μM, hydrocarbon degradation coupled to sulfate reduction is the dominating process over methanogenesis [54]. Sulfate-reducing microorganisms are phylogenetically diverse and can be found within the Proteobacteria, Firmicutes, Nitrospira and Thermodesulfobacteria, as well as in the Crenarchaeota and Euryarchaeota [55]. If sulfate is absent as electron acceptor, many sulfate-reducers can switch their metabolism to fermentative oil degradation, producing short chain fatty acids, molecular hydrogen and carbon dioxide [56,57]. For example, members of the genera Desulfovibrio, Desulfotomaculum and Archaeoglobus can grow with sulfate as electron acceptor or as fermenters in association with methanogens when sulfate is depleted [56,58–61]. Fermentation of hydrocarbons is thermodynamically only feasible when coupled to methanogenesis depleting both hydrogen and acetate [22,59,62–68]. Thus, methanogenic oil degradation is always a syntrophic process, where different members of the microbial community perform different steps in an overall metabolic process which cannot be fulfilled by a single member alone [69]. In addition, methane can be generated by acetoclastic methanogens disproportionateing acetate to CO2 and methane or by methylotrophic methanogenesis [70]. In fact, most of the biological methane generated in oil reservoirs originates from acetoclastic methanogenesis as indicated by stable isotope signatures [71]. Syntrophic interactions in oil reservoirs are not confined to a specific phylogenetic group of prokaryotes [56,59,63,72]. The two bacterial phyla Proteobacteria and Firmicutes and the three classes Archaeoglobi, Methanomicrobia and

| phylum / class               | order / genus                  | metabolic capacities                                                                    | references |
|------------------------------|--------------------------------|-----------------------------------------------------------------------------------------|------------|
| Proteobacteria / Gammaproteobacteria | Alteromonadales / Marinobacter | syntrophic alkane degraders                                                             | [63]       |
| Proteobacteria / Delaprotobacteria | Syntrophobacteriales / Smithella | syntrophic fatty acids and alkane degraders in association with methanogens             | [64]       |
| Proteobacteria / Desulfovibrionales / Desulfovibrio | Clostridales / Desulfomaculum | metabolically versatile, sulfate respiration and syntrophic alkane fermenters in association with methanogens | [56,66]   |
| Firmicutes / Clostridia | Clostridiales / Clostridium | association with methanogens                                                             | [56,61]   |
| Firmicutes / Archaeobacteria | Archaeoglobales / Archaeoglobus | sulfate-reducing archaea and syntrophic fermentative alkane degrader in association with acetotrophic methanogens | [59,72]   |
| Euryarchaeota / Methanomicrobia | Methanomicrobales / Methanoculleus | hydrogenotrophic methanogens                                                             | [56,73]   |
| Euryarchaeota / Methanomicrobia | Methanococcales / Methanoseta | aceticlastic methanogens                                                                  | [56,73]   |
| Euryarchaeota / Methanobacteria | Methanobacteriales / Methanobacterium | hydrogenotrophic methanogens                                                             | [72]       |
Methanobacteria affiliated to Euryarchaeota, are mostly involved in syntrophic interactions (Table 1) [56,63,72–75]. Many Proteobacteria are known to be syntrophic alkane degraders, e.g. members of the genera Marinobacter and Smithella have been highly enriched in methanogenic oil-degrading cultures [63,68,72,73,76]. Members of the genus Syntrophus can degrade alkanes and fatty acids in syntrophic association with methanogens [64,72]. As methanogenic and fermentative microorganisms are strongly dependent on each other, they are frequently organized in close vicinity to each other in order to provide a rapid exchange of electrons by diffusion of hydrogen or formate [67]. Furthermore, an electron exchange by direct interspecies electron transfer has been discovered; Geobacter metallireducens transfers electrons directly to Metanosaeta harundinacea during methanogenic degradation of ethanol, presumably by nanowires [77,78]. In addition, inorganic, electrically conductive particles inside a biofilm matrix can support interspecies electron transfer [79]. Thus, we suggest that the methanogenic degradation of oil mainly takes place in mutualistic microbial consortia organized in biofilms, where fermenting microbes transfer electrons either directly or indirectly to the methanogens.

Anthropogenic impacts – injection water

Oil production is the major anthropogenic factor influencing microbial communities in oil reservoirs. This includes drilling, flooding, hot steam and water injections, all of which lead to a high potential of invasion of external microorganisms into the original microbial communities [9,24,29]. Water injections are necessary in secondary oil production stages to increase reservoir pressure. The amount of injected water depends on the reservoir pressure, well age or water progressing within the reservoir. Oil companies use different types of injection waters consisting of either seawater, fresh water or recycled formation water. Offshore fields are mostly supplied with seawater [24,80] whereas in other oil fields groundwater [81] or surface water [30] are used. In some reservoirs, injection waters are enriched with chemicals or nutrients in order to manipulate the indigenous microbial community. For instance, nitrate and nitrite injections are used to suppress reservoir souring by microbial H2S production. Oxygen injections can stimulate the aerobic hydrocarbon metabolism and mobilize the oil within the well by lowering the interfacial tension between oil and water phase through biosurfactant producing microbes or changes in the oil matrix [82]. Alternatively, fermentative bacteria and carboxylate injection lead to the generation of acids, gases and solvents, which increases oil output, so called enhanced oil recovery (EOR) [8,31]. Water injections decrease the temperature of the oil field and build up a temperature gradient. The injection volume also affects the chemical composition of the production water, as it decreases the concentrations of magnesium, potassium, nitrate, nitrite and sulfate [24]. Production water is a byproduct of oil production and has been transported through the oil phase and pumped to the surface; it can be a mixture of formation and injection water and can contain particles and soluble compounds from oil [11,83] (Fig. 1). Two comparative studies have demonstrated higher concentrations of ammonium and fatty acids in formation water compared to production water [24]. Produced fluids with less than 10% injection water content did not have significant influence on microbial composition and metabolic potential. In contrast, fluids with a higher injection water cut indicated that the community composition and metabolic potential can be altered by the water composition. A close correlation was calculated between the relative abundance of the genus Flexistipes, family Deferrribacteres and the proportion of injected seawater and the concentrations of magnesium, potassium, nitrate, nitrite, and sulfate. Epsilonproteobacteria and Gammaproteobacteria were isolated in greater abundance from sample wells with the highest water injection rate [24]. Several studies have reported a relationship between the chemical composition of the oil reservoirs and the operational taxonomic units (OTUs) found therein. In Algerian oil reservoirs, production waters revealed significant correlations between the relative abundance of bacterial OTUs or phyla and Cl− and K+ ions. However, it is not clear if this correlation is causative. It may well be that the real causes for microbial community differences are for example differences in water content and structure of the reservoir and that the ion composition is just an indication of geological differences. Significant differences between microbial community composition of production and injection waters were observed for waters from Algerian oilfields and the offshore Halfdan oil field in the Danish North Sea. The Algerian oilfield injection water was richer in cells and dominated by bacteria, whereas the production water contained ten times fewer cells and was dominated by Archaea [24,81]. This difference indicates a trivial correlation between oil degradation processes in the methanogenesis-dominated reservoir and the microbial community composition in the production water.

Oil quality is determined by the degree of biodegradation and physical processes during oil production such as water injection or phase fractionation explained above. Those processes lead to lower concentrations of specific isomers, hydrocarbons, sulfur-, oxygen- and nitrogen-containing compounds [84,85] and an increase in oil viscosity, metals and microbial metabolites such as organic acids or sulfur compounds. Biodegraded oil reservoirs typically consist of oil-water emulsified fluids and systematic gradients built by different oil components [8,24]. For instance, isoprenoids and n-alkanes concentration decrease towards the OWTZ as they are degraded faster than aromatic compounds [11,86]. There, the degradation of oil is also controlled by the nutrient availability in the individual reservoir [8]. In contrast to many oil reservoirs, the bulk water contained in oil of the Pitch Lake in Trinidad and Tobago revealed that concentrations of essential nutrients, such as 95 mg/L ammonia and 5 mg/L phosphate, were not growth-limiting [27] demonstrating again that conditions within the oil phase allow biodegradation [67].

Abiotic factors – temperature, pH, and salinity

The geology of an oil reservoir determines the temperature, pH and salinity, which influence the composition and metabolic activity of the indigenous microbiota. Temperature is one of the most important factors determining microbial community composition in oil reservoirs [1,3,8,10,24,29,81]. Temperature increases by about 2–3 °C per 100 m of depth, which means that the effects of depth and temperature are closely related [3,81]. Generally, temperature is higher in reservoirs during primary production before injection, compared to similar reservoirs where water injections cool down the reservoir during secondary production [9,24]. The maximum temperature for hydrocarbon degradation in oil reservoirs is generally accepted to be around 82 °C [3,88]. The extreme solvent stress of the oil increases with elevated temperature and most likely the integrity of the cell membranes suffers. A study detected hyperthermophilic microorganisms in reservoirs with well temperatures up to 131 °C [80]. However, as the real conditions in the habitat could not be determined, it is highly unlikely that the organisms really thrived at that temperature in situ. So far, the record in hyperthermophilic growth is at 95 °C by the bacterium Aquifex pyrophilus and at 113 °C by the archaeon Pyrolobus fumarii, which of course did not take place in the presence of hydrocarbons [89]. Therefore, the detection of life at 131 °C is questioned by the indirect estimation of the oil temperatures and the so far known temperature maxima of microbes [10,80,81,90].

Nevertheless, highest microbial diversity has been found at moderately hot reservoirs with temperature of around 55 °C [91]. As everywhere in the environment, oil reservoirs harbor microorganisms with different temperature preferences (Table 2). Nitrospira, Aridibacteria and Acidobacteria were only detected in high-temperature oil reservoirs above 50 °C. Most Gammaproteobacteria, like Firmicutes, Thermotogae and Thermodesulfbacteria, showed a higher relative abundance in high-temperature oil reservoirs above 50 °C. Spirochaetes, Synergistetes, Chloroflexi, Marinobacterium, Paracoccus, Donghiella and Planctomycetes
Bacteria and archaea typically associated with low-temperature (< 50 °C) or high-temperature (≥ 50 °C) petroleum reservoirs.

| temperature optimum | phylum / class | order / genus | reference |
|---------------------|---------------|--------------|-----------|
| ubiquitous          | Proteobacteria / Epsilonproteobacteria | Campylobacterales / Arcobacter | [29] |
|                     | Proteobacteria / Epsilonproteobacteria | Campylobacterales / Sulfitospirillum | |
|                     | Proteobacteria / Gammaproteobacteria | Pseudomonadales / Pseudomonas | |
|                     | Proteobacteria / Alphaproteobacteria  | Rhizobiales / Rhizobium | |
|                     | Proteobacteria / Alphaproteobacteria  | Spingomonadales / Spingomonas | |
| only > 50 °C        | Crenarchaeota / Thermoprotei          | Fervidicoccales | [9] |
|                     | Euryarchaeota / Halobacteria          | Halobacteriales | |
|                     | Euryarchaeota / Halobacteria          | Halof Bereutae | |
|                     | Thaumarchaeota / Nitrosophrithia      | Nitrosophrithes / Nitrosophrith | |
|                     | Nitrospira / Nitrospira               | Nitrospira / Nitrospira | |
|                     | Crenarchaeota / Thermoprotei          | Sulfolobales | |
|                     | Proteobacteria / Deltaproteobacteria  | Syntrophobacterales / Thermoanforhabadus | [93] |
|                     | Euryarchaeota / Thermoplasmata        | Thermoplasmatales | [9,31] |
|                     | Crenarchaeota / Thermoprotei          | Thermoproteales | [9] |
|                     | Acidobacteria                         | Archaeoglobales | [9] |
| mostly > 50 °C      | Euryarchaeota / Archaeoglobi          | Archaeoglobales | [8,9,29] |
|                     | Firmicutes / Bacilli                  | Bacillales / Anaerobacillus | [29] |
|                     | Firmicutes / Bacilli                  | Bacillales / Bacillus | |
|                     | Firmicutes / Clostridia               | Clostridales / Thermosynortha | |
|                     | Euryarchaeota / Halobacteria          | Halobacteriales / Halogeometric | [31] |
|                     | Proteobacteria / Hydrogenophilalia    | Hydrogenophilales / Tepidophilus | [29] |
|                     | Thermotogae / Thermotogae             | Kosmotox | |
|                     | Euryarchaeota / Methanobacteria       | Methanobacterales / Methanothermalbacter | [29,31,94,95] |
|                     | Euryarchaeota / Methanomicrobia       | Methanocellales / Methanocellae | [31] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanococcus | [29] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanocalculus | [29,31] |
|                     | Euryarchaeota / Methanomicrobia       | Methanosaetales / Methanosaeta | [29] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanomyklovorans | [31] |
|                     | Nitrospira / Nitrospira               | Nitrospira / Thermodesulfobacter | [29] |
|                     | Proteobacteria / Alphaproteobacteria  | Rhodospirillales / Tisrella | |
|                     | Deinococcus / Thermus / Deinococci    | Thermales / Thermus | [8,10] |
|                     | Firmicutes / Clostridia               | Thermococcales / Thermococcus | [8,9,24,29,31] |
|                     | Euryarchaeota / Thermoprotei          | Thermoplasmatales / Thermopyromonas | [31] |
|                     | Actinobacteria / Thermophilae         | | [29] |
|                     | Bacteroidia / Bacteroidia             | | [24] |
|                     | Deferribacteres / Deferribacteres     | | [29] |
|                     | Firmicutes / Betaproteobacteria       | | [29] |
|                     | Proteobacteria / Deltaproteobacteria  | | [29] |
|                     | Tenericutes / Mollicutes              | | |
|                     | Thermodesulfobacteria                 | | |
| mostly < 50 °C      | Actinobacteria / Actinobacteria       | Actinomycetes / Microbacterium | [29] |
|                     | Actinobacteria / Actinobacteria       | Actinomycetes / Dietzia | |
|                     | Actinobacteria / Actinobacteria       | Actinomycetes / Rhodococcus | |
|                     | Proteobacteria / Gammaproteobacteria  | Aleronomadales / Marinobactera | |
|                     | Crenarchaeota / Thermoprotei          | Desulfuracocales | [9] |
|                     | Euryarchaeota / Methanobacteria       | Methanobacterales / Methanobacterium | [31,95,96] |
|                     | Euryarchaeota / Methanomicrobia       | Methanocellales | [9] |
|                     | Euryarchaeota / Methanomicrobia       | Methanococcales / Methanococcus | [29] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanomicrobium | [8,9,95,96] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanococcus | [29] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanocalculus | [29] |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanocalculus | | |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanocellae | | |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanolina | | |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanosarcinales | | |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanosarcinales | | |
|                     | Euryarchaeota / Methanomicrobia       | Methanomicrobiales / Methanolobus | | |
|                     | Proteobacteria / Alphaproteobacteria  | Rhodobacterales / Dohbicola | |
|                     | Proteobacteria / Alphaproteobacteria  | Rhodobacterales / Hyphomonas | |
|                     | Proteobacteria / Alphaproteobacteria  | Rhodobacterales / Paracoccus | |
|                     | Bacteroidetes                          | | [31,97] |
|                     | Chloroflexi                            | | [9] |
|                     | Planctomycetes                         | | [31] |
|                     | Proteobacteria                         | | [9] |

were more frequently detected in oil reservoirs below 50 °C. The archaea Halofaeacales, Thermoproteales, Sulfolobales, Nitrosophrithae, Halobaterales, Fervidococcales and Thermoplasmatales have been detected exclusively in high-temperature oil fields above 50 °C. Thermo- coccales and Archaeoglobales are known as thermophilic lineages and have frequently been isolated from oil reservoirs above 70 °C [24,29,92]. Methanobacteriales (e.g. Methanothermalbacter), Thermo- coccales (e.g. Thermococcus), Methanococcales and Archaeoglobales were most abundant in high-temperature oil fields [9]. Methanosarcinales, Methanomicrobiales (e.g. Methanococcusulcum and Methanolina),
Desulfurococcales and Methanocellales were mostly isolated from oil reservoirs below 50 °C.

Cai et al. investigated four production wells comprising a range of 1620 m–2470 m depth and 35.5 °C–69.0 °C [1]. They found an increasing relative abundance of genes related to the degradation of aromatic compounds (naba, HBH, and poba), carbon cycling and metabolism of other organic compounds with decreasing temperature and depth of oil-containing stratum. Stress response (heat shock), antibiotic resistance, and sulfur metabolism associated genes decreased with decreasing temperature [1].

Taken together, a correlation between functional gene occurrence and reservoir temperature has already been detected in nature. Oil degradation is highest at lower temperatures and reservoirs are more or less sterile at temperatures above 80 °C. Temperature is one of the major factors influencing microbial community composition and function in oil reservoirs producing trends on a genus level but not always on an order level. In general, it can be concluded that Proteobacteria (Alpha-, Gamma-, and Epsilonproteobacteria) and Euryarchaeota are ubiquitous in oil reservoirs across all temperature ranges. Sulfate-reducing bacteria (SRB) thrive from 4-85 °C [9]. Hence, no general predictions can be made on phylum or class level based on the oil reservoir temperature. On order and genus level, however, we can see clear temperature preferences as some orders, most of them archaea, were only isolated from high temperature reservoirs. Thus, they may serve as indicators for determination of in situ reservoir temperature. However, a general prediction of microbial community composition based on temperature alone is still not possible.

In oil reservoirs, salinity concentrations range from almost fresh- to salt-saturated water. Even though salinity and pH have been much less examined than temperature, they also have a high impact on microbial communities in oil by affecting growth and limiting bacterial activity. It was found that Clostridia correlated with low salinity of 3.8%, while Petrotoga and Desulfotomaculum species were mostly found in samples with a higher salinity of 7.2% [24]. It was suggested that hydrocarbon-degradation by Desulfotomaculum species may occur even under relatively high salinity conditions [24]. The amount of microbes isolated from oil fields decreased with increasing reservoir salinity above 10% [10]. Sulfate-reducing bacteria where found to resist wide ranges of salinity from 0 to 17% [9]. Manipulating the salinity of the injection water during oil-production to NaCl concentrations above 12% inhibits microbial H₂S production [8]. The analysis of two different pits from the La Brea Tar Pits in Los Angeles indicated that site-specific differences in salinity were highly correlated with microbial community structures within the asphalt [26]. Salt concentrations in oil reservoirs affected methanogenic oil biodegradation as hydrogenotrophic methanogenesis from CO₂ with H₂ was only measured up to a salt concentration of 9%, in situ [86,98] (Table 3).

The in situ pH values of oil reservoirs typically range from 3 to 7 [3]. Sulfate-reducing bacteria where not only found to resist wide ranges of salinity but also a wide range of pH values, from 4 to 9.5 [9]. A site-specific correlation between pH and microbial community structures was detected for two different pits from the La Brea Tar Pits in Los Angeles [99]. A study across 22 geographically separated oil reservoirs in China showed that Alphaproteobacteria, Deltaproteobacteria and Actinobacteria were most abundant in neutral to alkaline reservoirs with pH values between 7.0 to 8.2. *Pseudomonas* correlated with decreasing pH value of formation brine in the range of 5.5 to 7.6. *Gammaproteobacteria*, *Betaproteobacteria* and *Epsilonproteobacteria* preferred even more acidic environments and were detected in reservoirs with pH values of 5.5 to 6.5 [29] (Table 3).

**Viruses in oil reservoirs**

Viruses are known to have a major impact on microbial communities and their ecology [1,102–108]. By lysing their bacterial hosts, bacteriophages cause the release and turnover of nutrients such as proteins and nucleic acids [105,107]. Lysis can also result in changes in the bacterial community composition known as the ‘killing the winner’ hypothesis [105,106,109], meaning that host-specific predators (viruses) attack a bacterial population if the bacterial density increases over a certain threshold abundance. It thus prevents a species from emerging and maintains the coexistence of all species in the system [110]. ‘Killing the winner’ models predict that density- and frequency-dependent viral predation suppresses rapidly growing hosts, which leads to increasing host diversity [111]. Nevertheless, phages can also integrate into the host’s genome as prophages (lysogeny). The ‘piggy-back-the-winner’ model predicts relationships between virus-like-particles and host densities. The main advantage for the phage lies in continuous proliferation by the regular host cell growth and division, without killing the host [111,112]. Prophages protect the microbial cells from new infections by closely related phages. Due to the protection from lysis and other infections, prophages can drive bacterial evolution by transfer of genetic information between multiple hosts and promote thereby an increased diversity [107,111–113]. The gene transfer can affect the capacity for biofilm formation, the abilities of hydrocarbon-degradation, antibiotic resistance or the virulence in a positive or a negative way [103,114].

To date, the natural occurrence of bacteriophages and their interactions with bacteria in natural oil reservoirs has not been studied in much detail. As far as we are aware, no viruses have been directly isolated from an oil reservoir. Only studies at a genomic level have revealed hints of the presence of viruses. Oil-water mixture samples from a production well of the water-flooded Chinese Qinghai oilfield were compared in taxonomic and functional compositions of the microbial communities in the oil and water phases by pyrosequencing and application of a GeoChip4.0 [1]. In that study, 38 of 40 detectable virus genes were found. Three of the detected genes showed significant differences in abundance between crude oil and water phase. Holin type 3 for bacterial lysis was more abundant in the oil phase, while the host recognition T2 type and the sliding clamp T4 for replication were both greater in the water phase. Because of the higher abundance of phage genes in the water phase, it was hypothesized that microbes are protected from phages by the oil phase [1]. Yet, holin type 3 abundance was higher in oil than in water phase, indicating phage-interactions and bacterial lysis directly within the oil phase [1]. As a paradigm of life, microorganisms can only live in a water phase. Thus, microbes in the oil phase are either physically partitioned into the oil during the production process, where they cannot live, or they are present in microdroplets of water dispersed in the oil. In the latter case, they would again be subject to viruses if these are present in the droplet. Another genomic study on *Thermococcus sibiricus* isolated from oil concluded that the oil environment is poorly invaded by bacteriophages because they only found a single CRISPR containing 24 repeat spacer units. However, it is known that other species of the order Thermococcales harbor multiple CRISPR loci carrying more repeat spacer units [115].

The studies presented have shown that viruses occur in oil reservoirs. However, questions concerning their ecological importance and the extent to which they shape and control microbial communities and processes remain to be elucidated. Studies on oil-contaminated waters such as spills and plumes and the correlated bioremediation processes propose a phage-driven microbial loop [105,116]. The authors proposed that phages ensure a persistent nutritional biomass turnover enabling bacterial hydrocarbon degradation [117,118]. We could not find any support of either ‘killing the winner’ or ‘piggyback-the-winner’ processes in natural oil reservoirs in the literature indicating an open field for ecological research.

**Conclusion**

Microbial oil degradation in deep subsurface oil reservoirs mainly takes place at the so-called oil-water transition zone (OWTZ) or oil-water interface. Even, if the OWTZ is a degradation hotspot, we propose...
that microbial oil degradation also takes place in small water-saturated parts of the rock containing actively living microbes or even in the thin water film of water wet reservoirs. Thus, biodegradation is distributed in a gradient through the entire oil field starting from the OWTZ and following the water content to the top of the reservoir. Therefore, the water inclusions should be considered as having a notable impact on overall oil degradation process in the deep subsurface.

Water samples from oil reservoirs obtained by pumping comprise a foamy mixture of oil, formation or injection water, and gas. We propose to examine both the water and the emulsified water within the oil phase of a sample to get a better picture of the entire community present in an oil reservoir. However, production water samples cannot provide information about the real distribution of the microorganisms in the deep biosphere but may provide insight into which organisms are involved in oil degradation.

Another important factor are syntrophic interactions between different microorganisms. Often, planktonic microorganisms do not have access to both electron donor and electron acceptor as prerequisites for microbial energy conservation, especially fermenting bacteria and methanogenic archaea. Therefore, we suggest that the methanogenic degradation of oil mainly takes place in mutualistic microbial consortia organized in biofilms where fermenting microbes transfer electrons either directly or indirectly to the methanogens. In laboratory experiments, many oil-degrading enrichment cultures and isolates build biofilms on the surfaces of alkane phases or PAH’s. Since known advantages of biofilms include protection against toxic compounds and desiccation and syntrophic electron transfer between fermenting organisms and methanogenic archaea, we propose that life in deep subsurface oil reservoirs is arranged predominantly in biofilms.

An important influence regarding degradation rates of crude oil is reservoir temperature, with most inhabited reservoirs ranging from mesophilic to thermophilic conditions. The largest microbial diversity occurs at moderate temperatures of up to 55 °C, where higher metabolic activity and increased abundance of genes involved in carbon cycling and the degradation of aromatic and other organic compounds occurs. Above ~ 80 °C, oil reservoirs are considered to be sterile.

Oil reservoir temperature gives us an idea of microbial temperature preferences on a genus level but not always on an order level and so far no general predictions can be made about the phylum or class level. Some organisms may serve as indicators for in situ reservoir temperature determination. However, general predictions on microbial community composition based on temperature alone are not feasible. Viruses could be another important factor in oil reservoirs. Regarding the ‘killing the winner’ and the ‘piggyback-the-winner’ hypotheses, viruses could have an impact on shaping microbial communities and function, but no concrete evidence from oil reservoirs has been provided thus far.

Oil reservoirs provide an exceptional habitat for microorganisms, influenced by abiotic and biotic factors. Over the last decades, knowledge on the oil microbiome has grown but the function of the microorganisms described and the principles of the microbial oil degradation process still constitute open questions.

Funding sources

This work was supported by the European Research Council (ERC) [grant number 666952-EcOILogy] and the German Research Foundation (DFG) [grant number BR 5493/1-1].

Conflict of interest

The authors declare no conflict of interest.

References

[1] Cai M, Nie Y, Chi CQ, Tang YQ, Li Y, Wang XB, et al. Crude oil as a microbial seed bank with unexpected functional potentials. Sci Rep 2015;5:16657.
[2] Silva TR, Verde LCL, Neto EVS, Oliveira VM. Diversity analyses of microbial communities in petroleum samples from Brazilian oil fields. Int Biodeter Biodegr 2013;81:57–70.
[3] Magot M, Ollivier B, Patel BK. Microbiology of petroleum reservoirs. Antonie Van Leeuwenhoek 2000;77:103–16.
[4] Turhan I, Hachanaoglu E, Soytas U. Oil prices and emerging market exchange rates. Emerg Mark Financ Tr 2013;49:21–36.
[5] Head IM, Jones DM, Larster SR. Biological activity in the deep subsurface and the origin of heavy oil. Nature 2003;426:344–52.
[6] Liebensteiner MG, Tsesmetzis N, Stams AJ, Lomans BP. Microbial redox processes in deep subsurface environments and the potential application of (per)chlorate in oil reservoirs. Front Microbiol 2014;5:428.
[7] Timmis KN, Genity T, Van Der Meer JR, de Lorenzo V. Handbook of hydrocarbon and lipid microbiology. Berlin: Springer; 2010.
[8] Youssef N, Elshahed MS, McInerney MJ. Viral and bacterial diversity in oil fields: culprits, viruses could have an impact on shaping microbial communities and function, but no concrete evidence from oil reservoirs has been provided thus far.

Oil reservoirs provide an exceptional habitat for microorganisms, influenced by abiotic and biotic factors. Over the last decades, knowledge on the oil microbiome has grown but the function of the microorganisms described and the principles of the microbial oil degradation process still constitute open questions.

Funding sources

This work was supported by the European Research Council (ERC) [grant number 666952-EcOILogy] and the German Research Foundation (DFG) [grant number BR 5493/1-1].

Conflict of interest

The authors declare no conflict of interest.

References

[1] Cai M, Nie Y, Chi CQ, Tang YQ, Li Y, Wang XB, et al. Crude oil as a microbial seed bank with unexpected functional potentials. Sci Rep 2015;5:16657.
[2] Silva TR, Verde LCL, Neto EVS, Oliveira VM. Diversity analyses of microbial communities in petroleum samples from Brazilian oil fields. Int Biodeter Biodegr 2013;81:57–70.
[3] Magot M, Ollivier B, Patel BK. Microbiology of petroleum reservoirs. Antonie Van Leeuwenhoek 2000;77:103–16.
[4] Turhan I, Hachanaoglu E, Soytas U. Oil prices and emerging market exchange rates. Emerg Mark Financ Tr 2013;49:21–36.
[5] Head IM, Jones DM, Larster SR. Biological activity in the deep subsurface and the origin of heavy oil. Nature 2003;426:344–52.
[6] Liebensteiner MG, Tsesmetzis N, Stams AJ, Lomans BP. Microbial redox processes in deep subsurface environments and the potential application of (per)chlorate in oil reservoirs. Front Microbiol 2014;5:428.
[7] Timmis KN, Genity T, Van Der Meer JR, de Lorenzo V. Handbook of hydrocarbon and lipid microbiology. Berlin: Springer; 2010.
[8] Youssef N, Elshahed MS, McInerney MJ. Viral and bacterial diversity in oil fields: culprits, viruses could have an impact on shaping microbial communities and function, but no concrete evidence from oil reservoirs has been provided thus far.

Oil reservoirs provide an exceptional habitat for microorganisms, influenced by abiotic and biotic factors. Over the last decades, knowledge on the oil microbiome has grown but the function of the microorganisms described and the principles of the microbial oil degradation process still constitute open questions.

Funding sources

This work was supported by the European Research Council (ERC) [grant number 666952-EcOILogy] and the German Research Foundation (DFG) [grant number BR 5493/1-1].

Conflict of interest

The authors declare no conflict of interest.

References

[1] Cai M, Nie Y, Chi CQ, Tang YQ, Li Y, Wang XB, et al. Crude oil as a microbial seed bank with unexpected functional potentials. Sci Rep 2015;5:16657.
[2] Silva TR, Verde LCL, Neto EVS, Oliveira VM. Diversity analyses of microbial communities in petroleum samples from Brazilian oil fields. Int Biodeter Biodegr 2013;81:57–70.
[3] Magot M, Ollivier B, Patel BK. Microbiology of petroleum reservoirs. Antonie Van Leeuwenhoek 2000;77:103–16.
[4] Turhan I, Hachanaoglu E, Soytas U. Oil prices and emerging market exchange rates. Emerg Mark Financ Tr 2013;49:21–36.
[5] Head IM, Jones DM, Larster SR. Biological activity in the deep subsurface and the origin of heavy oil. Nature 2003;426:344–52.
[6] Liebensteiner MG, Tsesmetzis N, Stams AJ, Lomans BP. Microbial redox processes in deep subsurface environments and the potential application of (per)chlorate in oil reservoirs. Front Microbiol 2014;5:428.
[7] Timmis KN, Genity T, Van Der Meer JR, de Lorenzo V. Handbook of hydrocarbon and lipid microbiology. Berlin: Springer; 2010.
[8] Youssef N, Elshahed MS, McInerney MJ. Viral and bacterial diversity in oil fields: culprits, viruses could have an impact on shaping microbial communities and function, but no concrete evidence from oil reservoirs has been provided thus far.

Oil reservoirs provide an exceptional habitat for microorganisms, influenced by abiotic and biotic factors. Over the last decades, knowledge on the oil microbiome has grown but the function of the microorganisms described and the principles of the microbial oil degradation process still constitute open questions.

Funding sources

This work was supported by the European Research Council (ERC) [grant number 666952-EcOILogy] and the German Research Foundation (DFG) [grant number BR 5493/1-1].

Conflict of interest

The authors declare no conflict of interest.

References
reservoirs. Int Biodegr Biodegrad 2017;12:170–85.

[10] Roling WF, Head IM, Larner SR. The microbiology of hydrocarbon degradation in subsurface petroleum reservoirs: perspectives and prospects. Res Microbiol 2003;154:521–8.

[11] Larner S, Wilhelmsen A, Head I, Koopmans M, Aplin A, Di Primio R, et al. The controls on the composition of biodegraded oils in the deep subsurface—part 1: bio-degradation rates in petroleum reservoirs. Org Geochem 2003;34:601–15.

[12] Kobayashi H, Endo K, Sakata S, Mayumi D, Kawaguchi H, Ikarashi M, et al. Phylogenetic diversity and microbial community structures in the crude-oil, large-insoluble-particle and formation-water components of the reservoir fluid from a non-aerated high-temperature petroleum reservoir. J Biosci Bioeng 2012;113:204–13.

[13] Ridley CM, Voordouw G. Aerobic microbial taxa dominate deep subsurface cores from the Alberta oil sands. FEMS Microbiol Ecol 2018;94:fiy073.

[14] Sierra-García IN, de Oliveira VM. Microbial hydrocarbon degradation: efforts to understand biodegradation in petroleum reservoirs. Biodegradation-engineering and biotechnology. InTech; 2013.

[15] Abbasmehdi H, Gray M, Foght JM. Influence of adhesion on aerobic biodegradation and bioremediation of liquid hydrocarbons. Appl Microbiol Biotechnol 2012;91:1693–703.

[16] Nazina T, Ivanova A, Golubeva O, Belyaev S, Ivanov M. Occurrence of sulfate and iron-reducing bacteria in stratal waters of the Romashkinskoe oil field. Microbiology-New York 1995;64:203–8.

[17] Nazina T, Shestakova N, Pavlova N, Tantarki Y, Ivoslov V, Khiametdinov M, et al. Functional and phylogenetic microbial diversity in formation waters of a low-temperature carbonate petroleum reservoir. Int Biodegr Biodegrad 2013;81:71–81.

[18] Sempel K, Weslake D. Characterization of iron-reducing Alteromonas putrefaciens strains from oil field fluids. Can J Microbiol 1987;33:366–71.

[19] Greene AC, Patel BK, Sheehy AJ. Deferribacter thermophilus gen. nov., sp. nov., a novel thermophilic iron-reducing bacterium isolated from geothermal systems. Int J Syst Bacteriol 1997;47:505–9.

[20] Feng W-G, Liu J-F, Gu J-D, Mu B-Z. Nitrate-reducing community in production water of three oil reservoirs and their responses to different carbon sources revealed by nitrate-reducing encode gene (napA). Int Biodegr Biodegrad 2015;65:1081–6.

[21] Lovley DR, Chapelle FH. Deep subsurface microbial processes. Rev Geophys 1995;33:365–81.

[22] Zengler KH, Rossello-Mora R, Michaelis W, Widdel F. Methane formation from long-chain alkanes by anaerobic microorganisms. Nature 1999;401:266–9.

[23] Chilingar GV, Yen TF. Bitumens, asphalts, and tar sands. Developments in petroleum science. Amsterdam: Elsevier Science; 1978. p. 331.

[24] Vigneron A, Aloup EB, Lemans RP, Kyrpides NC, Head IM, Toumazet N. Succession in the petroleum reservoir microbiome through an oil field production lifecycle. ISME J 2017;11:214–54.

[25] Korenblum E, Souza DB, Penna M, Sedlin L. Molecular analysis of the bacterial communities in crude oil samples from two brazilian offshore petroleum platforms. Int J Microbiol 2012;2012:156537.

[26] Kim JS, Crowley DE. Microbial diversity in natural asphalts of the rancha La breta tar pits. Appl Environ Microbiol 2007;73:5664–9.

[27] Meckenstock RU, von Netzer F, Stump C, Luersd T, Himmelberg AM, Hertkorn N, et al. Oil biodegradation. Water droplets in oil are microhabitats for microbial consortia enriched from oil reservoir production waters. Front Microbiol 2014;4:919.

[28] Golyshin PN, Chernikova TN, Abraham WR, Lunsdorf H, Timmis KN, Yakimov MM. Oleiphilaceae fam. nov., to include Oleiphilus messinensis gen. nov., sp. nov., a novel marine bacterium that obligately utilizes hydrocarbons. Int J Syst Evol Microbiol 2002;52:99–108.

[29] Johnsen AR, Karlson U. Evaluation of bacterial strategies to promote the bioavailability of polycyclic aromatic hydrocarbons. Appl Microbiol Biotechnol 2004;63:452–9.

[30] Klein B, Bouriat P, Goulas P, Grimaud R. Behavior of Marinobacter hydrocarbonivorans in oil fields. Appl Environ Microbiol 1999;65:2697–702.

[31] Whiticar MJ, Faber E, Schoell M. Biogenic methane formation in marine and freshwater environments—Co reduction vs acetate fermentation isotope evidence. New Biotechnol 2019;49:1–9.
M. Pannekem et al.

Geochim Cosmochim Ac 1986;50:693–709.

Piceno YM, Reid FC, Tom LM, Conrad ME, Bill M, Hubbard CG, et al. Temperature and injection water source influence microbial community structure in four Alaskan North Slope hydrocarbon reservoirs. Front Microbiol 2014;5:409.

Fowler SJ, Toth CR, Gieg LM. Community structure in methanogenic enrichments provides insights into syntrophic interactions in hydrocarbon-impacted environments. Front Microbiol 2016;7:562.

Sierra-Garcia IN, Delligaeeze BM, Santos VP, Chaves BM, Capilla R, Santos Neto EV, et al. Microbial diversity in degraded and non-degraded petroleum samples and comparison across oil reservoirs at local and global scales. Extremophiles 2017;21:211–29.

Wang LY, Gao CX, Mbadinga SM, Zhou L, Liu J, Gu JD, et al. Characterization of an alkane-degrading methanogenic enrichment culture from production water of an oil reservoir after 274 days of incubation. Int Biodeter Biodegrad 2015;105:44–50.

Qin QS, Feng DS, Liu PF, He Q, Li X, Liu AM, et al. Metagenomic characterization of candidatus Smithella cisterna strain MB2,1, a syntrophic alkane-degrading Bacteria, Enriched from the Shengli Oil Field. Microbes Environ 2017;32:234–43.

Rotaru AE, Shrestha PM, Liu FH, Shrestha M, Shrestha D, Embree M, et al. A new model for electron flow during anaerobic digestion: direct interspecies electron transfer to Methanosaeta for the reduction of carbon dioxide to methane. Energy Environ Sci 2014;7:408–15.

Kouzuma A, Kato S, Watanabe K. Microbial interspecies interactions: recent findings in syntrophic consortia. Front Microbiol 2015;6:477.

Kaster EM, Bonanet K, Beal H, Kjeldsen-Illerensen G, Brakstad OG. Characterisation of culture-independent and -dependent microbial communities in a high-temperature offshore chalk petroleum reservoir. Antonie Van Leeuwenhoek 2009;96:423–39.

Lenci N, Inceroli O, Kebbecho-Gana S, Gana ML, Liouro M, Servais P, et al. Diversity of microbial communities in production and injection waters of algerian oilfields revealed by 16S RNA gene amplicon 454 pyrosequencing. PloS One 2013;8:e66586.

Kowalewski E, Rurslätten I, Steen K, Bedtger G, Torseter O. Microbial improved oil recovery—biological induced wetting and interfacial tension effects on oil production. J Petro Sci Eng 2006;52:275–86.

Dahle H, Garshol F, Madsen M, Birkeland NK. Microbial community structure analysis of produced water from a high-temperature North Sea oil field. Antonie Van Leeuwenhoek 2008;93:37–49.

Fedork PM, Westlake DW. Microbial degradation of alkyl carbazoles in Norman Wells crude oil. Appl Environ Microbiol 1984;47:858–62.

Huang HP, Bowler BJF, Zhang ZW, Oldenburg TBP, Lar T. Influence of bio-degradation on carbanzole and benzoncarbaze distributions in oil columns from the Liaohe basin, NE China. Org Geochem 2003;33:951–69.

Head IM, Gray ND, Larser SR. Life in the slow lane; biogeochemistry of biodegraded petroleum containing reservoirs and implications for energy recovery and carbon management. Front Microbiol 2014;5:566.

Wang LY, Ke WJ, Mbadinga SM, Zhou L, Liu JF, Gu JD, et al. Characterization of bacterial communities in production and injection waters of algerian oil reservoirs using pyrosequencing and clone library approaches. Appl Microbiol Biotechnol 2009;82:6115–28.

Head IM, Jones DM, Roling WF. Marine microorganisms make a meal of oil. Nat Rev Microbiol 2013;11:147–58.

Shapiro OH, Kushmaro A, Brenner A. Bacteriophage predation regulates microbial abundance and diversity in a full-scale bioreactor treating industrial wastewater. ISME J 2010;4:327–36.

Weinbauer MG, Rassoulzadegan F. Are viruses driving microbial diversity and evolution? Environ Microbiol 2004;6:1–11.

Weitz JS, Poisot T, Meyer JR, Flores CO, Valverde S, Sullivan MB, et al. Phage-bacteria coevolution as a driver of ecological and evolutionary processes in microbial communities. FEMS Microbiol Rev 2014;38:916–31.

Ravot G, Magot M, Olivier B, Patel BK, Ageron E, Grimont PA, et al. Haloanaerobium congolense sp. nov., an anoxic, moderately halophilic, thiosulfate- and sulfur-reducing bacterium from an African oil field. FEMS Microbiol Lett 1997;147:81–8.

Belyakova EV, Rozanova EP, Borzenkov IA, Tourova TP, Pusheva MA, Lysenko EV, et al. Methanosarcina barkeri. Appl Environ Microbiol 2014;80:4599–605.

Bhupathiraju VK, McInerney MJ, Woese CR, Tanner RS. Haloanaerobium kushneri sp. nov., a novel methanogenic bacterium from an oil-producing well. FEMS Microbiol Lett 1997;147:51–6.

Gray ND, Sherry A, Larter SR, Ermann M, Leyris J, Liengen T, et al. Biogenic methanol production in formation waters from a large gas field in the North Sea. Extremophiles 2009;13:511–9.

Kim JS, Crowley DE. Microbial diversity in natural asphalt of the rancho la brea tar pits. Appl Environ Microbiol 2007;73:4579–91.

Lu Z, Deng Y, Van Nostrand JD, He Z, Voordeckers J, Zhou A, et al. Microbial gene transfer to Methanosarcina barkeri. Appl Environ Microbiol 2007;73:4579–91.

Weinbauer MG, Rassoulzadegan F. Are viruses driving microbial diversity and evolution? Environ Microbiol 2004;6:1–11.

Weitz JS, Poisot T, Meyer JR, Flores CO, Valverde S, Sullivan MB, et al. Phage-bacteria coevolution. Aquat Microb Ecol 1997;13:19–27.

Head IM, Jones DM, Roling WF. Marine microorganisms make a meal of oil. Nat Rev Microbiol 2013;11:147–58.

Ravot G, Magot M, Olivier B, Patel BK, Ageron E, Grimont PA, et al. Haloanaerobium congolense sp. nov., an anoxic, moderately halophilic, thiosulfate- and sulfur-reducing bacterium from an African oil field. FEMS Microbiol Lett 1997;147:81–8.

Bhupathiraju VK, McInerney MJ, Woese CR, Tanner RS. Haloanaerobium kushneri sp. nov., a novel methanogenic bacterium from an oil-producing well. FEMS Microbiol Lett 1997;147:51–6.

Gray ND, Sherry A, Larter SR, Ermann M, Leyris J, Liengen T, et al. Biogenic methanol production in formation waters from a large gas field in the North Sea. Extremophiles 2009;13:511–9.

Kim JS, Crowley DE. Microbial diversity in natural asphalt of the rancho la brea tar pits. Appl Environ Microbiol 2007;73:4579–91.

Lu Z, Deng Y, Van Nostrand JD, He Z, Voordeckers J, Zhou A, et al. Microbial gene transfer to Methanosarcina barkeri. Appl Environ Microbiol 2007;73:4579–91.

Weinbauer MG, Rassoulzadegan F. Are viruses driving microbial diversity and evolution? Environ Microbiol 2004;6:1–11.

Weitz JS, Poisot T, Meyer JR, Flores CO, Valverde S, Sullivan MB, et al. Phage-bacteria coevolution. Aquat Microb Ecol 1997;13:19–27.

Head IM, Jones DM, Roling WF. Marine microorganisms make a meal of oil. Nat Rev Microbiol 2006;4:73–82.

Lu Z, Deng Y, Van Nostrand JD, He Z, Voordeckers J, Zhou A, et al. Microbial gene functions enriched in the Deepwater Horizon deep-sea oil plume. ISME J 2012;6:451–60.

McGeeny TJ, Forbell BW, McKew BA, Sanni GO. Marine crude-oil biodegradation: a central role for interspecies interactions. Aquat Biosyst 2012;8:1–15.