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Blue economy: A new era of petroleum microbiology in a changing climate

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Abstract: The productivity and health of our ocean hold some good solutions to the world's challenges in socio-economy. However, climate change and waste discharge are changing the marine capacity to buffer human impacts, further challenging the marine industry, primarily in offshore oil and gas, shipping, and fishery operations. These encourage the blue economy, a sustainable development approach to utilize marine resources. Petroleum microbiology dealing with microbes that can respond, degrade, and alter crude oils, offers an unprecedented opportunity to achieve the knowledge- and science-based blue economy. However, the new-era petroleum microbiology for supporting the blue economy has yet to be systematically discussed. This review introduces the climate change impacts on key marine industrial sectors, highlights the critical role of advanced petroleum microbiology in supporting sustainable development, and offers insight into the challenges and future research opportunities in availing of petroleum microbiology for benefiting our marine environment and responsible economic growth.

Keywords: blue economy, sustainability, climate change, petroleum microbes, bioproduction, carbon neutrality

Introduction

The ocean covers approximately 70.8% of the surface of our living planet, and more than half of the world's population lives within 50 miles of the coast [1]. Faced with a shortage of land use and energy exhaustion, the ocean holds unprecedently untapped opportunities to deliver resources (e.g., foods, fuels, and other value-added chemicals), making it an indispensable role in economic development. The marine industry has recently contributed U.S. $2.5 trillion to the global economy annually, and the asset value of the ocean has been estimated at $24 trillion [2]. However, ocean-generated values are threatened by cumulating human activities. The irrational excavation and exploitation of marine resources have led to increasingly severe environmental and climate issues.

Main marine industrial sectors, e.g., offshore oil and gas, shipping, and fishery, have inevitably caused mounting emissions of greenhouse gas (GHG) and discharges of various pollutants, deteriorating marine wealth and health [3–5]. For example, in Canada, offshore oil and gas is the largest GHG emitter, accounting for 27% of total emissions in 2020, with 179 megatons of CO_2 equivalent emitted [6,7]. The GHGs and oily wastes are generated over the whole lifecycle, including exploration, production, and oil spills. Shipping, accounting for 90% of the world's trade, enables 1.97 billion dead-weight tons of capacity [8]. The emissions of GHGs from shipping have increased from 977 million tons in 2012 to 1076 million tons in 2018, sharing nearly 3% of global anthropogenic emissions [9,10]. The fishery and seafood industry provides value-added sources to support human life; meanwhile, seafood catching and processing have generated massive contaminants like plastics [11,12] and crude fishery waste materials [13,14].

Global climate change has further deteriorated the marine industry in most cases. Although the ocean is incredibly effective at absorbing exceeding 90% of heat and 25% of CO_2 caused by human activities, its changed properties resulting from climate change, have led to decreased marine productivity [15,16]. To combat climate change and to realize the sustainable usage of marine resources, the United Nations Sustainable Development Goal 14 (UN SDG 14), i.e., life below water, highlights the need to conserve and sustainably use the oceans, seas and marine resources for sustainable development [17,18]. In addition, the High-Level Panel for a Sustainable Ocean Economy (Ocean Panel) has been initiated by building momentum for a sustainable ocean economy (i.e., blue economy)—a version for effective protection, sustainable production, and equitable prosperity [19,20]. These have put forward a new Ocean Action Agenda, which aims to transform the marine industry into a knowledge- and science-based blue economy.

The deployment of biotechnology has demonstrated an environmentally friendly pathway in the marine industry. The subsection petroleum microbiology dealing with microorganisms that can respond, degrade, and alter crude oils (i.e., petroleum microbes), plays a critical role in the blue economy [21,22]. Previously known petroleum biotechnology was limited to oil-related activities, such as oil reservoir monitoring, enhanced oil recovery, and bioremediation [23]. With the economic and environmental demand, the genetic and physiological of petroleum microbes are widely excavated, leading the range of petroleum microbiology extending to the valorization of wastes [24], crude oil upgrading to generate clean fuels [25], and the mitigation of emerging contaminants [26], etc. These industrial applications highly lie in petroleum microbes with diverse functionalities for biotransformation and bioproduction.

The blue economy, which aims to utilize marine resources sustainably, is becoming incredibly pivotal, particularly under climate change conditions. As an essential aspect of biotechnology, petroleum microbiology has been developed to a new era to provide promising solutions supporting the blue economy. However, existing knowledge of advanced petroleum microbiology in sustainable development has yet to be reviewed and discussed. For this endeavor, this study first introduces climate change impacts on the marine industry. State-to-art knowledge of the roles of petroleum microbiology in supporting the blue economy is then comprehensively summarized and prospected. This review paper also sheds light on the challenges and future developments of petroleum microbiology-based sustainable biotechnologies.

Climate change impacts on marine industry

Marine industry

The marine industry is all commercial ocean-based activities containing well-established (e.g., offshore oil and gas, fishery, shipping, port activities, tourism, marine manufacturing) and emerging (e.g., renewable energy, marine biotechnology) industrial sectors [27]. These sectors provide products and services ranging from food and transportation to energy and health, generating value important to local, coastal, and national economies. As the fundamentals of the marine industry, offshore oil and gas, shipping, and fisheries account for the most important ones and contribute significantly to the social economy. Meanwhile, these activities also inevitably cause severe environmental and climate impacts.

Offshore oil and gas industry Oil and gas are critically important in our daily life: they are used not only to power our cars and heat our houses but also to turn into countless products such as plastics, clothes, tires, etc. They are still the main components of the current world's energy structure, accounting for more than half of the global energy usage [28,29]. The offshore oil and gas industry is activities related to exploring and producing oils from the oil and gas reservoirs and the actions to mitigate generated wastes and oil spills.

During reservoir exploration, the geophysical survey is first conducted to predict the nature of the source. Seismic survey is widely applied by releasing and detecting high-pressure sound waves' bursts [30]. The exploratory drilling will then be performed to collect information on the quantities of the oils and the geological parameters [31]. Afterward, the development drilling and production will be committed to extracting and recovering the oil from the reservoirs. To enhance oil recovery, secondary and tertiary (i.e., enhanced oil recovery) will be conducted by injecting water and floodings with chemical/biological additives, respectively [32]. Meanwhile, the oil reservoir souring, the most harmful microbial process during oil production, would be intensified due to the enrichment of these corrosion-related bacteria like sulfate-reducing bacteria (SRB), threatening marine infrastructures [33].

Various oily wastes will be generated, such as drilling cuttings [34] and produced water [35]. Besides, GHGs are massively emitted from exhaust engines, gas flaring, well-testing, and oil recovery operations. Marine oil spills, the release of liquid petroleum hydrocarbons in marine environments, may happen accidentally along offshore oil and gas operations, from drilling and production to transportation, due to inappropriate human activities and extreme weather conditions. The largest offshore oil spill disaster in U.S. history, the Deepwater Horizon oil spill, has caused more than the spilling of 3.19 million barrels of crude oil, 6800 dead birds and mammals, and nearly $40 billion for the cleanup [36].

Shipping Shipping is the most efficient and cost-effective means of transportation for most goods, facilitating commerce and helping to create prosperity among nations and peoples. International Maritime Organization (IMO), the U.N. specialized agency responsible for the safety and security of shipping and the prevention of marine and atmospheric pollution, has highlighted that the contribution of shipping to climate change primarily lies in that most shipping vessels burn heavy fuel oil (HFO), a dirty fuel that releases GHGs like CO_2, sulfur dioxide, nitrogen oxides, and tiny dust particles named black carbon. In the Arctic, the black carbon settles on sea ice, absorbs light, and converts the light to heart, accelerating sea ice melt and increasing atmospheric warming [37]. The Intergovernmental Panel on Climate Change (IPCC) has called to reduce its use to help achieve climate targets [38]. In this context, transitioning from dirty to cleaner fuels is highly demanded to realize sustainable shipping.

Fishery Fishery, including industrial capture fisheries, marine aquaculture, and processing, provides more than 17% of animal protein worldwide [39]. From 1990 to 2018, the ocean produced nearly 200 million tons of seafood annually. The global fish and seafood market is projected to grow at a Compound Annual Growth Rate (CAGR) of 7.4% in the forecast period of 2023–2028 [24].

Fishing gear makes up nearly 10% of the world's marine plastic pollution, with 640,000 tons being dumped and discarded in the ocean yearly [40]. Those "ghost gear" have been threatening marine life and ecosystems.

For example, about 300 sea turtles were found dead in 2019 because of entanglement in ghost gear off the coast of Oaxaca, Mexico [41]. The weathering of these plastics would release myriads of micro- and nano-plastics, inducing severe eco-toxicological impacts by entering the food web [42]. Besides, plastic wastes also contribute to the emission of GHGs, from the breakdown of plastics by weathering processes like sunlight and heat to the interference with the ocean's ability to sequester carbon, such as slowing down plankton photosynthesis [43].

Algae (e.g., seaweed), fish (e.g., different species of salmon, cod, tuna), and marine invertebrates (e.g., shrimps, oysters, crabs, lobsters, scallops) account for most of the seafood market [24]. The cultivation of algae does capture the CO_2 via their photosynthesis and produces a high content of food. However, as people become wealthier, they want to eat more meat other than algae [44]. For fish and invertebrates, the processing results in plenty of waste discharged. It was reported that only approximately 30% was used for human consumption [45]. If not properly managed, the fishery waste disposals would reduce the oxygen level in the seawater, burial or smothering of living organisms, and introduce disease to marine ecosystems [46]. The large stream of fishery wastes, including fish heads, scales and fins, and viscera, as well as the seashells and viscera, deserve recovery and valorization.

Climate change impacts

The ocean, acting as one of the two most important carbon sinks (the other is vegetation), accumulates and stores carbon for an indefinite period to remove atmospheric CO_2. In response, the excessive absorption of CO_2 in the global ocean has altered the seawater environment, such as ocean acidification, ocean warming, reduced sea ice, rising sea level, reduced oxygen level, and increased frequency and intensity of extreme weather events [44]. These alterations will decrease marine productivity and eventually affect marine activities (Figure 1).

Ocean acidification The increased acidification of seawater has a broad impact on the marine industry, primarily by altering the geological process, inducing more corrosion, and affecting marine organisms [47]. Ocean acidification influences the formation of source rocks (the rock that contains the organic matter, such as dead plants and animals in the sedimentary basins) and maturation (the process that transforms organic matter into hydrocarbons) [48]. The seismic surveys that rely on the ability of sound waves to penetrate different rock formations and layers will be more challenging to obtain accurate subsurface information. The instability of the seabed and surrounding sediment layers caused by ocean acidification also increases the technical difficulty and risk of drilling and production activities [49]. Besides, ocean acidification induces more corrosion and reduces the lifespan of subsea infrastructures, ships, and fishing gear [50]. It was also widely reported that higher acid would decrease seafood quality (e.g., shellfish, lobsters) for ocean food productivity [51].

Ocean warming Over the past 50 years, global temperature has risen appropriately by 1.2°C. In the Arctic, it has risen nearly 3°C [52]. In the offshore oil and gas industry, warmer temperatures cause subsidence or uplift of the seabed, altering the structures of oil reservoirs and the surrounding rocks [53]. The changes in ocean currents resulting from ocean warming will also induce the movement of drilling platforms and lead to shipping with increased voyage times and higher costs [54]. Besides, these corrosion-related microbes would be more active in warmer conditions to stimulate the erosion of the associated infra-

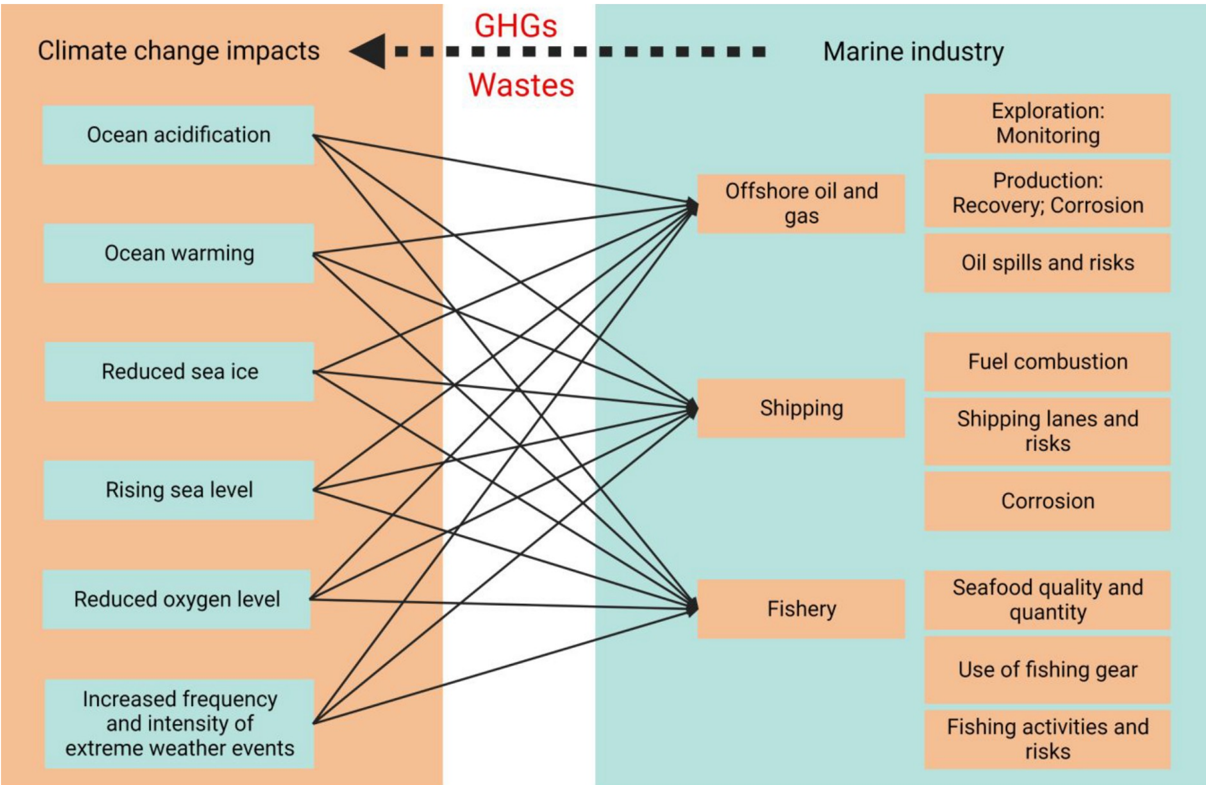

Figure 1 Climate change impacts on the marine industry.

structures. Additionally, ocean warming will change the fish distribution and abundance, the timing of reproductive cycles, and zooplankton for fish health and survival [55]. Some fish species would migrate to cooler waters, influencing the productivity of fishing grounds. For example, the Pacific anchovy, previously found from California to British Columbia, is increasingly observed migrating to and spawning in its Canadian range [56]. Besides, the disrupted timing of reproductive cycles may negatively affect the survival and growth of some fish's offspring [57,58]. The warmer temperature would also make nutrient producers, the copepods, smaller with lower fats and nutrients for feeding fish [59].

Reduced sea ice The sea ice can reflect sunlight into space, provide habitats for various marine species, and regulate global climate. Reduced sea ice refers to the decrease in the extent, thickness, and duration of sea ice cover in polar regions. As a physical barrier, sea ice makes it difficult for oil companies to access and survey potential oil reserves beneath the ocean floor. The reduced sea ice within connected Arctic corridors would increase accessibility to previously unreachable offshore oil and gas reserves, opening new areas for exploration and production in the short term [60]. For shipping, on the one hand, the reduced sea ice opens up new lanes, potentially shortening transportation routes, allowing for faster and more efficient shipping, and reducing the burning of HFO and the cost of shipping. On the other hand, mounting melting sea ice may make shipping more dangerous, especially for large-scale commercial transportation [61]. The reduced sea ice can also lead to changes in wildlife habitats and migration patterns; for example, in the Arctic and Atlantic oceans, the reduced sea ice can alter the distribution and abundance of Arctic cod, the prey species for many predators like seals and whales, causing cascading effects on the Arctic food web [62].

Rising sea level Sea level rise refers to the increase in the average height of the ocean's surface relative to the land level due to the melting of glaciers and sea ice. The IPCC predicts that global sea levels will rise between 26 and 82 centimeters (10 and 32 inches) by the end of the 21st century [63]. The rising sea level can change the depth and areas for ocean activities and increase the risks of coastal flooding, making it challenging to conduct oil reservoir surveys, exploratory oil drilling, and production, particularly in the shallow waters near the coast. Some of the offshore drilling platforms may become partially or even completely submerged. Besides, the rising sea level changes the depth of shipping channels, making some shipping routes inaccessible to associated ports. For the fishery, rising sea level can cause the loss of important coastal and estuarine habitats such as mangroves, marshes, and seagrass beds [64,65]. They provide essential breeding, feeding, and nursery grounds for many fish species.

Reduced oxygen level The increased ocean temperature leads to decreased ability to hold oxygen. It creates a warm, low-oxygen surface water layer to prevent mixing with the more profound and colder water for oxygen exchange [66]. Besides, ocean acidification also decreases the ability of marine organisms to extract oxygen from the water [67]. The reduced oxygen level can induce more corrosion-related processes by providing corrosion-causing bacteria such as iron-oxidation, sulfate-reducing, and acid-producing bacteria with favorable conditions for growth and proliferation [68]. Reduced oxygen level also significantly impacts the fishery by changing marine species' distribution, behavior, abundance, and health [69]. These will make it more challenging to catch and harvest desired species and supply seafood for human consumption.

Increased frequency and intensity of extreme weather events The frequency and intensity of extreme weather events, such as hurricanes, typhoons, and high winds and waves, are dramatically elevated due to climate change. They endanger offshore oil reservoir surveys and operations, damage associated infrastructures and pipelines, and increase the risks of marine oil spills [70]. The high winds and waves also make it hard to maintain control of ships and increase the frequency of collisions with other ships or shore-based infrastructures.

Petroleum microbiology supporting blue economy

Various marine industrial sectors are intricately intertwined with climate change. Global climate change has been causing multitudinous impacts on the marine industry; Contemporaneously, the marine industry also deteriorates marine health and decreases its capacity for absorbing GHGs. Critical climate change impacts on the marine industry raise challenges and demand better solutions. To relieve and tackle the impacts on marine wealth and health, the blue economy, which aims to utilize marine resources sustainably, has been advocated. It demands the transition of the traditional exploiting approaches into sustainable practices, thereby maximizing the environmental and social-economic benefits [71].

Advanced technologies, primarily marine biotechnology tailored to the changing climate, should be developed to realize sustainable goals. Biotechnology uses living organisms and their enzymes to develop products or processes to assist in industrial and human activities [72]. Petroleum microbes are pivotal marine resources—their exploration and deployment would provide the solutions to facilitate sustainable marine industry development under climate change conditions. Petroleum microbiology is a branch of microbiology that deals with microorganisms that can respond, degrade, and alter crude oils. The demands for sustainable development have spawned a new-era petroleum microbiology to support the blue economy. In offshore oil and gas, petroleum microbes and associated products are used for oil reservoir monitoring, oil recovery, and oily waste remediation. These depend highly on the oil-degrading bacteria that can respond and degrade oil components and produce surface-active agents (i.e., biosurfactants) [73]. Beyond the oil and gas industry, the development of petroleum microbiology also highlights its role in upgrading fuel oils and producing advanced biofuels to decrease the generation of atmospheric pollution. Furthermore, recent studies also demonstrated the capacity of petroleum microbes to assist in the degradation of plastic wastes caused by the usage of fishing gear, as well as the valorization of fishery wastes to value-added bioproducts (named biorefinery) during seafood processing [74] (Figure 2). The crucial microbes with their specific characteristics supporting the marine industry are listed in Table 1.

Petroleum microbiology supporting offshore oil and gas industry

Well-established specialized microbial communities are populated in pristine oligotrophic marine ecosystems. The aphorism "everything is everywhere, but the environment selects" denotes that microbes can adapt to changing environments by assimilating specialized carbon and energy sources [99]. The petroleum biota is found in petroleum environments, and mounting petroleum microbes are detected and manipulated for engineering applications in the lifecycle of the offshore oil and gas industry.

Microbial monitoring Microbial processes, including biodegradation, methanogenesis, and souring, are essential in oil and gas reservoirs [100]. Biodegradation can enable the formation of lighter hydrocarbons in the reservoir. Therein, methanogens can use hydrogen and CO_2 to produce methane. The oil reservoir souring

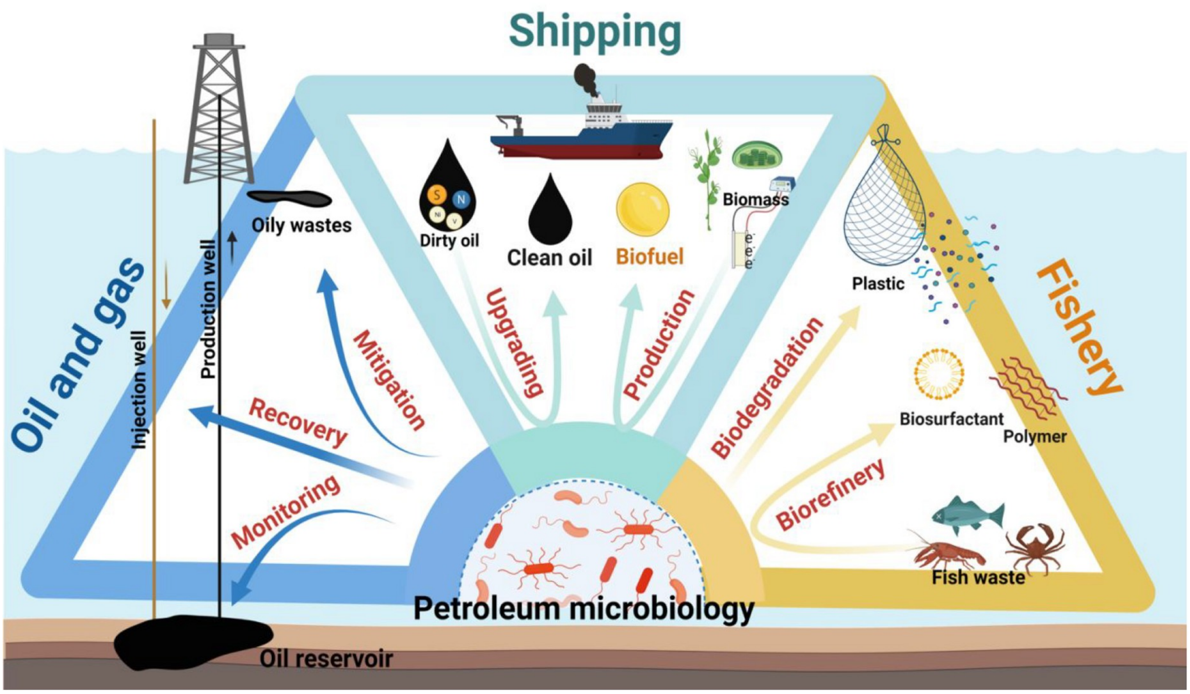

Figure 2 Petroleum microbiology supporting blue economy.

Table 1 List of crucial petroleum microbes (genus level) with their specific characteristics supporting the marine industry

Petroleum microbes	Characteristics for supporting the relevant marine industry
Alcanivorax	Offshore oil and gas: Boosting quickly when facing hydrocarbons—their monitoring can provide information on the oil reservoir and oil spills [73]; Producing biosurfactants (anionic glycolipids) for microbial-enhanced oil recovery [75]; Degrading alkanes via beta-oxidation pathway for the mitigation of oily wastes [26]. Fishery: Degrading synthetic polyesters and PE plastic wastes [76]; Synthesizing PHA polymers for waste valorization [77].
Desulfomicrobium	Offshore oil and gas: Notorious sulfate-reducing bacteria—their monitoring can provide information on corrosion-related oil activities [33].
Pseudomonas	Offshore oil and gas: Producing biosurfactants (rhamnolipids) for microbial-enhanced oil recovery [78]; Degrading petroleum hydrocarbons for the mitigation of oily wastes [79]. Shipping: Biodenitrogenation of nitrogen heterocyclic compounds (e.g., carbazole and carbazone) and biodesulfurization of DBT for oil upgrading [80]; Acting as the platform to produce biofuels such as ethanol, butanol, and value-added hydroxy acids [81,82]. Fishery: Depolymerizing several plastics like PVC, PE, and PS [83]; Using wastes to synthesize various pharmaceutical and agricultural bioproducts, such as PHA polymers and biosurfactants, for sustainable production [84].
Rhodococcus	Offshore oil and gas: Producing biosurfactants (trehalolipids) for microbial-enhanced oil recovery [85]; Degrading petroleum hydrocarbons for the mitigation of oily wastes [86]. Shipping: Biodenitrogenation and biodesulfurization of heavy oils supporting oil upgrading [87]; Producing biodiesel [88]. Fishery: Degrading plastics potential for the biodegradation of diverse plastics from genome-based observation [89]; Producing various products such as biosurfactants and triacylglycerol using fish wastes [90].
Bacillus	Offshore oil and gas: Producing biosurfactants (lipopeptides) for microbial-enhanced oil recovery [91]; Degrading petroleum hydrocarbons and secreting biosurfactants to add to the mitigation of oily wastes [92]. Shipping: Secreting cytochrome C reductase as biocatalyst for heavy oil biodemetallization [23]; Producing isoprenoid-based biofuels via genetic modification [93,94]. Fishery: Biodegradation of diverse plastics such as PE and PS [95]; Producing various valuable chemicals such as biosurfactants, gelatin, 5-aminolevulinic acid, and PHA polymers using fish wastes [96,97].
Cycloclasticus	Offshore oil and gas: Degrading aromatics in petroleum hydrocarbons for the mitigation of oily wastes [73]. Fishery: Degrading plastics such as polyethylene terephthalate (PET) [98].

primarily caused by dissimilatory sulfate reduction will cause corrosion [101]. As microbial community compositions are shaped when facing diverse environmental stresses, their monitoring can provide valuable information to support the sustainable development of the oil and gas industry. Microbial community analysis of the reservoir fluids can give information to help predict the reservoir conditions, such as the presence of the organics and the temperature and pressure gradients [102]. This can further the understanding of the oil reservoirs and provide a valuable tool to support oil reservoir surveys beyond the geophysical seismic survey.

In addition, microbial monitoring can also provide information for managing microbial corrosion in the oil production system. For example, the microbial community's enrichment of SRB, such as *Desulfomicrobium*, indicates a high degree of corrosion [103]. Since the acidification of the ocean caused by climate change can further strengthen corrosion, microbial monitoring is increasingly important to expand our understanding of corrosion and benefit the decision-making in oil and gas production.

Microbial-enhanced oil recovery During oil production, primary recovery involves the natural flow of oil from the reservoir, recovering nearly 5%–15% of oils. In comparison, secondary recovery consists of injecting water or gas to increase pressure and displace additional oil to recover an extra 20% to 40% of the original oil in place [104]. Enhanced oil recovery can provide economic benefits and aims to extract the large inaccessible portion of oils trapped in reservoirs' pore space beyond the primary and secondary recovery stages. In enhanced oil recovery, the injection of chemicals can reduce the viscosity and improve the mobility of oils for recovery. However, these chemicals, including chemical surfactants, synthetic polymers, and alkaline chemicals, pose negative impacts and generate hazardous wastes threatening the indigenous ecosystems [105].

Microbial-enhanced oil recovery is a biotechnical approach by injecting specific microbes, nutrients, and/or biosurfactants to improve the fluidity of highly viscous oils [106]. The injection of enriched microbes can accelerate the breakdown of heavy crude oils and decrease the viscosity. The challenge of this approach highly depends on the survival and capacity of the injected microbes to adapt to the oil reservoir's native environmental conditions. Nutrient injection involves the addition of nutrients, such as nitrogen and phosphate, to stimulate the growth and activity of indigenous microbes. But inevitably, some unfriendly microbes like corrosion-related bacteria may also be enriched. Diverse petroleum microbes can produce biosurfactants. For instance, trehalose lipids generated by *Rhodococcus*, lipopeptides (or surfactin) generated by *Bacillus*, and rhamnolipids generated by *Pseudomonas* are well-known biosurfactants for industrial and environmental applications [107]. Their injection can decrease the surface tension between liquids and solids and between different liquids and form stable emulsions under diverse environmental conditions. Besides, they can further enhance the microbial biodegradation process in the reservoirs by forming lighter components and changing the properties of crude oils. Meanwhile, biosurfactants can also act as eco-friendly anti-corrosion substances by damaging the formed biofilms and inhibiting the growth of corrosion-related bacteria [108].

Mitigation of oily wastes Oily wastes are generated in multiple steps of the offshore oil and gas industry, primarily containing drilling cuttings, produced water, and spilled oils. Diverse hydrocarbon-degrading bacteria can respond quickly and degrade the crude oil components naturally. Some can only degrade the crude oils' sole part, and others can transform multiple components. For example, the prestigious obligate marine hydrocarbon degrader, *Alcanivorax*, would boost and majorly degrade alkanes quickly [26], while the genus *Cycloclasticus* is responsible for the degradation of aromatics [73]. The *Pseudomonas*, *Rhodococcus*, and *Bacillus* can simultaneously degrade diverse organic components, including alkanes and aromatics [70]. The microbial responses and metabolic networks have been well studied for a long time, and it is widely recognized that microbial-mediated natural attenuation is essential for mitigating discharged oily wastes.

In addition, biosurfactants have also been widely used to mitigate oily wastes. These biosurfactants have been mixed with various additives like solvents or particles to improve associated performance. Various environmentally friendly bioproducts, like biodispersants, biodemulsifiers, and bioherders, have been formulated accordingly to replace the traditional toxic chemical ones. The application of biodispersants can enhance the oil dilution and biodegradation in the seawater and act as a promising strategy in oil spill response [109]; biodemulsifiers can accelerate the separation of oil from water, thereby supporting the recovery of oils from the oily wastes [110]; bioherders can support in-situ burning in the oil spill response through accumulating the floating oils to oil slicks with a higher thickness (2–3 mm) [85]. Given the strong capacity of oil biodegradation and biosurfactant production by petroleum microbes, biological approaches can dramatically support the sustainable mitigation of oily wastes. Hence, excavating critical petroleum microbes and developing ideal and cost-friendly biosurfactants are crucial to sustainable oil recovery and mitigation.

Petroleum microbiology for generating clean fuels supporting sustainable shipping

Worldwide, petroleum-based fuels account for more than 70% of the energy used by transportation [111]. In the U.S. transportation sector, nearly 9.5 million barrels of petrol are consumed per day. Relevant marine fuel types include HFO, liquid natural gas (LNG), marine diesel fuel (MDO), marine gas oil (MGO), and biofuel, among which HFO is the most used one due to the low cost and historically lax regulatory requirements [112]. To realize sustainable shipping, the IMO launched a new regulation on the amount of sulfur allowed in global shipping restricted by 0.5% in 2020 [113]. For this endeavor, the fundamental approach is to transform the usage of dirty HFO into cleaner fuel oils. The LNG consists of clean-burning properties; however, it is difficult for vessels to run on and is an expensive choice for ship operations. MDO, the very-low sulfur fuel with a max sulfur emission of 0.5%, and MGO, the ultra-low sulfur fuel with a max sulfur emission of 0.10%, can provide cleaner options as fuel oils in marine shipping. Biofuels refer to completely sulfur-free fuels made from renewable biomass sources, shielding the lights to serve as future shipping fuels. To generate green fuels supporting shipping, petroleum microbiology demonstrates the capacity for oil upgrading and the production of biofuels.

Oil upgrading Fuel oils such as HFO contain various impurities, especially sulfur, nitrogen, and metals. The burning of fuel oils containing high amounts of sulfur, nitrogen, and heavy metals would lead to the formation of harmful emissions. To decrease the impurities, oil upgrading is demanded, including desulfurization, denitrogenation, and demetallization [114].

Sulfur is typically composed of the third most abundant element, with nearly 0.05% to 5% in crude oil and up to 14% in heavy crude oils. Desulfurization is an approach used for reducing sulfur; therein, hydrodesulfurization is the currently most used petroleum refinery practice [115]. However, this approach is energy- and materials-consuming and can hardly realize the removal of sulfur to a very low level. Petroleum biotechnology provides a greener approach, utilizing the biodesulfurization pathways and enzymes to break down the organically bound sulfur [116]. For example, four enzymes involved in the complete removal of sulfur from dibenzothiophenes (DBT), named DBT monooxygenase (DszC), DBT-sulfone monooxygenase (DszA), flavin reductase (DszD), and 2-(2′-hydroxyphenyl) benzenesulfonic acid (HPBS) desulfurase (DszB) [117,118]. This system has been cloned and identified from multiple petroleum microbes, such as *Rhodococcus* and *Pseudomonas* [119].

Nitrogen accounts for about 0.3% of crude oils, with 75%–75% nonbasic compounds (e.g., indole and carbazone). The burning of carbon-bounded nitrogen contributes to the formation of nitric oxides. Similar to desulfurization, the removal of nitrogen can be achieved using high-pressure and high-temperature hydrotreating [120]. Biodenitrogenation, depending on the pathways for transforming nitrogen heteroaromatics, offers an environmentally friendly strategy [121]. The indole is easily biodegradable via bacterial oxygenase to form hydroxylated intermediates [122]. Carbazone, the major nitrogen compound in crude oils, is relatively resistant to bioconversion but can be biodenitrogenated via a complicated carbazole-degradative operon in petroleum microbe *Pseudomonas* sp. strain CA10 [123].

The presence of heavy metals such as iron, nickel, and vanadium in oils can cause increased corrosion, catalyst poisoning, and potential environmental pollution. Although the biodemetallization process is yet clearly understood, the prime step is the redox reaction and enzymatic hydrolysis. The enzyme chloroperoxidase in *Caldariomyces fumag* was reported to be able to remove nearly 20% of the nickel and vanadium from asphaltene in heavy crude oils [124]. The *Bacillus* can secrete cytochrome C reductase as biocatalysts for heavy oil biodemetallization [23].

Production of advanced biofuels Biofuels are the ideal alternatives to replace petroleum-based fuels in shipping. They are typically produced from renewable lignocellulosic biomass, photosynthesis, and bioelectrochemistry systems using diverse biofuel-producing microorganisms [24]. Two major biofuels, i.e., ethanol and biodiesels, are widely commercialized and may decarbonize marine transportation. According to the International Energy Agency (IEA), in April 2022, the cost of ethanol is estimated to be $0.8 per litter in the U.S. while $1.3 in Europe, and the price of biodiesel is nearly $2.0 in the U.S. while S1.7 in Europe [125]. Compared with diesel, which costs almost $1.1 in both the U.S. and Europe, biodiesel costs nearly two folds of diesel [126]. Although these biofuels have been commercialized and the global demand for biofuels is set to grow by 41 billion liters, or 28%, over 2021–2026 in the main case, their real-world applications are still challenging, considering the quality and price of the bioproducts are not superior to petroleum-based fuel oils for use in suitable transport engines.

The indicators, i.e., octane number and cetane number, show the quality of the hydrocarbons in the engine [127]. The octane number reflects the fuel's ability to resist compression in a combustion engine, while the cetane number measures the fuel's ignition quality. The types and hydrocarbons in fuels strongly affect their properties. For instance, the branching and unsaturation of hydrocarbons can increase the octane number, decrease the cetane number in fuels, and help prevent gelling at low temperatures to support shipping activities in cold regions [128]. The mixture and production of more and better biofuels are demanded for real-world usage.

Advanced biofuels, such as isoprenoids, fatty acids, higher alcohols and esters, and polyketides, are widely produced using model species such as *E. coli* and *Saccharomyces cerevisiae* by integrating and optimizing diverse metabolic pathways using synthetic biology and metabolic engineering manners [128]. However, these microbial hosts cannot feasibly perform in producing high amounts of biofuels since the products and intermediates are typically considered toxic to model hosts. For example, the bioproduct isoprenol is toxic to *E. coli* when reaching concentrations higher than 2% [129]. Further, the model species can only function in specific mild environments with limited external stress (e.g., temperature, salinity, and acidification). Taking *E. coli* as an example, when temperature decreases to 0°C, it can scarcely grow [130]; when salinity reaches that of seawater, it loses the colony-forming ability and dehydrates due to osmosis pressure [131]; acidification can induce stress and affect the bacterial survival and growth through interfering the DNA repair system (SOS) and heat shock-like responses [132]. Therefore, we believe harnessing marine petroleum microbes, mainly those tailored to the extreme conditions of nature, can arm biotechnology for the large-scale production of biofuels.

Petroleum microbes have existed in nature to degrade crude oils for a long time and evolve to endure diverse toxic components. For instance, *Pseudomonas putida* strains have both cellular export and hydrocarbon catabolism systems for their tolerant phenotype [84]. Successful and high-level production of fatty acid ethyl esters (23 g/L) and long-chain hydrocarbons (5 g/L) have been achieved by using the oleaginous actinobacterium *Rhodococcus opacus* as the microbial chassis [133], which can degrade a broad range of organics including toxic aromatics in petroleum [134]. In addition to tolerance to toxic products, petroleum microbes can also resist high salinity as they are distributed in coastal and marine environments [135]. The discovery and exploitation of petroleum microbial chassis with the capacity to tolerate extreme environmental pressures can decrease the risk of microbial contamination and shed light on future large-scale biofuel production.

Petroleum microbiology in sustainable fishery

In fishery activities, fishing gear significantly contributes to the world's ocean plastic pollution. Overfishing would lead to the overuse of fishing gear and exhausting fish resources. Further, during seafood processing, a massive stream of fishery wastes will be generated.

Petroleum microbiology is derived from oil-responding or oil-degrading bacteria. The plastics are typically refined from crude oils, indicating that petroleum microbes can also degrade the plastic wastes in the marine environment. In addition, developing cost-effective circular technologies for marine biomass/biowastes valorization into value-added products is imperative for sustainable economic goals. Here, we highlight the critical role of petroleum microbes in plastics biodegradation and the valorization of fishery wastes.

Mitigation of plastic wastes The global ocean acting as the pool has been receiving a diversity of plastic wastes. In the fishery industry, fishing gears like nets, lines, buoys, and containers are majorly made from polyethylene (PE), polypropylene (PP), polystyrene (PS), polycarbonate (PC), polyvinyl chloride (PVC), polyethylene terephthalate (PET), etc. [136]. Plastics are polymers, and the biodegradation of plastics primarily starts from microbial depolymerization and oxidation of the carbon chain [26]. Many petroleum microbes own the capacity (e.g., *Alcanivorax*, *Pseudomonas*, *Rhodococcus*, and *Bacillus*) as they can sufficiently metabolize the alkanes and aromatics in crude oils (Table 1).

The well-known obligate alkane-degrader *Alcanivorax*, has now been reported for degrading natural and synthetic polyesters and PE plastics [76]. The presumed degradation mechanism lies in the secretion of depolymerase enzymes and extracellular reactive oxygen species. In addition, the previously reported species with the capacity to degrade aromatics, such as *Bacillus*, can change the surface properties of PS plastics and initiate biodegradation [95]. These imply that the alkane- and aromatic-degrading petroleum microbes have a high potential to degrade the different types of plastic waste. The ocean has environmental resiliency to mitigate plastic waste. It may be because petroleum microbes have naturally existed for the degradation of hydrocarbons for a long time. These resources can also be further exploited for industrial applications in recycling plastic waste.

Valorization of fishery wastes Globally, nearly 35 million tons of fishery waste are discharged into the ocean annually, endangering our marine environments. These wastes, mainly derived from algae biomass, marine invertebrates (e.g., shells, viscera), and fish (e.g., head, bones, viscera), contain high properties of nutrients and carbon sources and can be considered secondary raw marine resources. Biorefinery can convert these so-called "worthless" residues into beneficial and valuable by-products. This win-win scenario can help protect our ocean and support the marine economy. Petroleum microbes enormously add to the valorization process and can help generate various high-value products, such as biosurfactants, natural polymers, fatty acids and oils, pigments, organic solvents, proteins, and other fermented products [24,74,137]. Here, we highlight two important products, i.e., biosurfactants and polymers, as they significantly support the marine industries and our daily lives.

Microbial production of biosurfactants is the natural process that oil-degrading bacteria would like to have more accessibility to and increase the bioavailability of crude oils [91]. Unsurprisingly, microbial utilization of hydrophobic compounds initiates the biosurfactant secretion engine. Still, some biosurfactant-producing bacteria can also produce biosurfactants under a broad range of carbon and nitrogen sources [138]. To realize the economic feasibility, the production of biosurfactants from fishery wastes should be hydrolyzed and then fermented. Till now, many biosurfactant products have been commercialized. For example, commercial rhamnolipids are produced by companies AGAE Technologies, Jeneil Biosurfactant, TensioGreen in the United States, and Biofuture in Ireland, with a retail price of nearly $629.5/kg [139]. The biosurfactants have many applications: in the oil and gas industry, they can enhance oil recovery and support oil spill response [109]; in the environmental field, they can stimulate soil flushing and remediation [91]; in the food industry, they are functional ingredients [140]; in the agricultural and biological field, they are antibiological chemicals for biocontrol [141]. Biosurfactants have a vast market and have a high potential to replace the traditionally used chemical surfactants in diverse areas. The biosurfactant market had a global market size valued at $3.99 billion in 2016 and reached $5.52 billion by 2022, at a CAGR of 5.6% [142].

The polymer can be made from seafood waste via chitin extraction, a natural polymer found in the shells of invertebrates such as shrimp and crabs. In addition, polymers can also be accumulated in the petroleum microbes. For instance, *Alcanivorax* can accumulate intracellular polymer-based carbon reservoirs to face the oligotrophic condition [143]. These polymers are typically polyhydroxyalkanoate (PHA), the raw material for manufacturing the most environmentally friendly emerging biodegradable plastics. If blended appropriately, PHA can potentially replace the traditionally used plastic gear to realize the circular economy in the fishery industry, although research is still in its infancy [144]. The associated cost-benefit analysis should be further conducted considering the economy, environment, and society. One case study taking the polylactic acid (PLA) production using biomass (i.e., cassava) as a feedstock shows that the cost includes the investment and production (e.g., materials and land cost), operation (e.g., reactor control and extraction), and wastes management (e.g., wastewater treatment and GHGs emission control), and the benefit includes the direct benefit (i.e., sale of the product) and the indirect benefit (e.g., the by-products and decrease of petroleum utilization and wastes generation impacts) [145]. Among these, the production step accounts for the highest cost and largest carbon emission footprint. In addition, another simulation study suggests that the complete replacement of fossil feedstocks with biomass (e.g., sugarcane) would reduce plastic-related carbon emissions by ~25% [146]. Since traditional plastic production consumes nearly 5%–7% of the global oil supply and released >850 million tonnes of CO_2 into the atmosphere in 2019, representing 2% of the global CO_2 output [147], switching existing processes to use the fish waste can further cut the cost and plastic-related emissions. The quantitative cost-benefit analysis is pivotal and deserves accurate calculation to benefit the full understanding and utilization of circular strategy in fishery industry.

Challenges and future developments

Marine industry developments highly contribute to the social economy by exploiting the wide range of valuable ocean resources. Meanwhile, related activities, primarily offshore oil and gas, shipping, and fishery operations, will inevitably emit a large stream of GHGs and wastes, threatening the ocean's health and wealth. Global climate change further deteriorates marine environments. It has caused ocean acidification, ocean warming, reduced sea ice, rising sea level, reduced oxygen level, and increased frequency and intensity of extreme weather events, making traditional industrial activities incredibly challenging. The new-era petroleum microbiology can support the sustainable use of marine resources; their future development will further benefit our environment, global climate, and economy. Here, we offer insight into the challenges and future research opportunities to exploit petroleum microbiology. Typically, the exploitation of petroleum microbes for industrial applications consists of three progressive steps: (1) the understanding of microbial information; (2) the robust microbial design; and (3) the design and integration of bioreactors that support the biological active environments for large-scale production (Figure 3).

Microbial information

Microbes can provide valuable information to help predict the environmental process in specific regions; meanwhile, a deep understanding of microbial regulation and functional genetic information can support

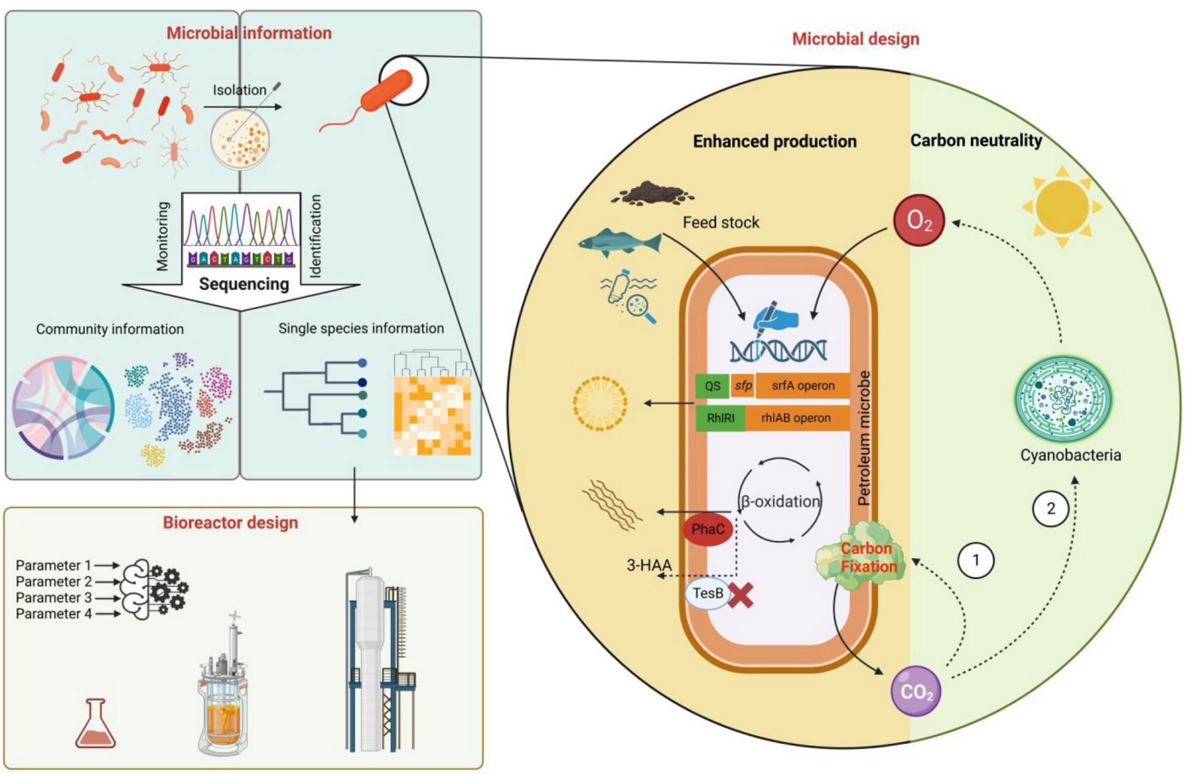

Figure 3 Challenges and future developments of petroleum microbiology to support blue economy.

microbial design. Knowing the microbial community composition and functions helps understand the conditions of the reservoir, microbial-induced corrosion, and microbial capacity for the mitigation of wastes and the production of bioproducts. Pivotal isolated petroleum microbes and associated metabolic pathways should be well clarified before rational microbial design for industrial applications.

Advanced genetic sequencing tools, especially amplicon sequencing, metagenomics, and metatranscriptomics, can disclose mysterious information on the microbial community composition, functions, and activities to support microbial monitoring and microbial-mediated natural attenuation. However, the in-depth knowledge, particularly the contribution of critical microbial species in a community, is still hysteresis. Through a metagenomic binning-centric process, the binned draft genomes or metagenome-assembled genomes (i.e., MAGs) can further display behaviors of the specific species with an unprecedented resolution. However, it may cause the possibility of missing important information from the non-binned database since not all the sequences can be clearly defined and integrated [73]. Also, more new microbial pathways and functions will be discovered as the database pools are enormously enlarged. These demand the complement and enrichment of the big database to support the new-era petroleum microbiology.

Prior to utilizing pivotal non-model petroleum microbes for industrial applications, isolation and characterization should be conducted first. Whole-genome sequencing can give information on microbial classification, identification, and critical pathways in waste biodegradation and bioproduct generation, benefiting the selection of microbial chassis. Given the advanced characterization tools, more promising petroleum microbes will be isolated to override the limitation of using model species for industrial applications. For example, the selection of petroleum microbes growing in low-temperature environments and with high industrial feasibility can save the energy consumed for maintaining mild temperatures.

Microbial design

Transforming the feedstocks from marine wastes to value-added products using petroleum microbes can provide a promising strategy in the blue economy. The isolation of species with environment-tailored metabolic pathways for robust degradation and production is the primary, but more importantly, the microbial engineering approaches (i.e., genetic-based engineering) can further strengthen the high-efficient cell factories. Besides the intensification of critical metabolic pathways, CO_2 is still inevitably emitted, demanding carbon-neutral microbial design.

Microbial design for enhanced bioproduct generation Petroleum microbes have superiorities over the model species due to their stress (e.g., toxic chemicals, temperature, salinity) tolerance and capacities of degrading marine wastes (e.g., oily and fishery wastes, and plastics) and producing value-added chemicals (e.g., biosurfactants, biopolymers). The development of synthetic biology offers an opportunity for optimizing microbial degradation and production processes, with the typical strategies lying in the three steps: (1) microbial chassis selection, (2) pathway design and optimization, and (3) tolerance engineering. Given that petroleum microbes have high tolerance as promising microbial chassis, it may save the step of tolerance engineering in this endeavor. Further, it is unusual to integrate exogenous biodegradation pathways or overexpress the specific degrading enzymes for real industrial applications, though several studies have highlighted that transplanting the exogenous pathways into the model species *E. coli* can realize the bioremediation of aromatics [148]. Since the petroleum microbes do have the strong capacity to degrade the petroleum, transplanting these pathways may be superfluous, as this work can be easily realized by chassis selection.

In contrast, the pathways to produce value-added chemicals deserve strong enhancement. Pathways for biosynthesizing well-known biosurfactants, e.g., lipopeptides and rhamnolipids, have been clearly illustrated and optimized. The biosynthesis of lipopeptides by marine *Bacillus* relies on the srfA operon that is composed of *srf*AA, *srf*AB, *srf*AC, and *srf*AD, plus the *sfp* gene coding the translational regulator [91]. In addition, the quorum sensing (QS) system also regulates cell density for biosurfactant production. Optimizing the promoters for srfA operon using constitutive promoters can override the limitation caused by QS system, realizing nearly four folds of production (from 0.07 g/L increased to 0.26 g/L) [149]. Meanwhile, the rhlAB operon regulated by RhlRI QS system produces rhamnolipids in *Pseudomonas* [78]. It has been reported the overexpression of *rhlAB* genes resulted in a noticeable increment (from 1.98 g/L increased to 2.87 g/L) [150].

Apart from that, the pathway for biosynthesizing biopolymers, such as the PHA in *Alcanivorax*, is regulated by PHA synthase (PhaC). The intermediate (R)-3-OH-Acyl-CoAs produced during β-oxidation is converted to either 3-HAA (3-hydroxy alkanoic acids) through the action of "TesB-like" acyl-CoA thioesterase or PHA through the act of PhaC [77]. The disrupting of "TesB-like" CoA can directly enhance the production of PHA from 0.018 to 2.56 g/L using octadecane as the carbon source. These have identified that rewriting metabolic pathways of petroleum microbes can improve microbial robustness for bioproduct production. However, the synthetic biological toolbox of non-model petroleum microbes lags behind it for model species. Genetic engineering of marine non-model species has received increasing attention recently. For the first time, Wei *et al*. [151] developed a base editing system for the marine *Roseobacter* clade bacteria, one of the most abundant bacteria accounting for nearly 20% of the bacterial communities in the ocean. This research opens a new avenue for marine biosynthesis and biorefinery, showing a high potential to enable the environmentally relevant non-model microorganisms for deployment in supporting the blue economy.

Microbial design for carbon neutrality Carbon neutrality means offsetting the generated CO_2 via carbon capture, storage, and conversion to achieve net zero carbon emission [152]. More than 120 countries globally have put carbon-neutral goals in diverse industrial areas. Taking the production of biosurfactants from oily wastes as an example, the production of biosurfactants to replace chemical surfactants was reported to have a low carbon footprint. The life cycle analysis showed that 1 metric tonne (Mt) of a typical ethoxylated surfactant replaced with 1 Mt of sophorolipid-based biosurfactant reduces CO_2 emissions by 1.5 Mt [153]. However, most of the strategies are generalizations and lack approaches to further upgrade generated CO_2. The microbial ability to assimilate CO_2 into biomass sets a clear approach to realizing carbon neutrality during the processes and reactions. Herein, we introduce two promising strategies to realize the recycling of CO_2: (1) incorporating carbon fixation pathways into heterotrophic petroleum microbes and (2) co-culturing with the photoautotrophic cyanobacteria.

In nature, there are many routes to fix CO_2, including the Calvin Benson (CB) reductive pentose phosphate cycle, reductive citric acid cycle (rTCA) cycle, reductive acetyl-CoA (Wood-Ljungdahl) pathway, 3-hydroxy propionate (3HP) cycle, 3-hydroxypropionate/4-hydroxybutyrate (3HP/4HB) cycle, dicarboxylate/4-hydroxybutyrate (DC/4HB) cycle, etc. [154,155]. The CB cycle is involved in the primary production process, whereby the key enzyme is RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase). It has been reported that the integration of RuBisCO followed by the long-term evolution can enable *E. coli* to produce biomass [156] and *Saccharomyces cerevisiae* to alleviate GHG emissions during the production of second-generation ethanol [157]. In addition, the overexpression of enzymes in the 3HP cycle can establish carbon fixation in *E. coli* [158]. However, the harness and selection of carbon fixation pathways still face many challenges to improve efficiency: (1) enzymes in routes (except for the CB cycle) have limited environmental tolerance as they only exist in extremely hot or acid conditions or the anoxic/anaerobic organisms; (2) CB cycle is widely distributed and studied in higher plants, algae, and cyanobacteria, but it is with low efficiency and high energy intensity to fix CO_2. It requires 9 mol ATP and 6 mol NAD(P)H for the fixation of 3 mol CO_2 [159]. The evolution of routes tailoring to petroleum microbes or the integration of more than one carbon fixation pathway may resolve the challenges, though the coexistence of two autotrophic ways in one species is quite rare [154]. Future fundamental knowledge and applied research can open the mind for genetically integrating high-efficient heterogeneous carbon fixation pathways into petroleum microbes.

Another approach to realizing carbon neutrality is using the co-culture with cyanobacteria. This approach is inspired by the natural ocean hydrocarbon cycle, whereby widely distributed CO_2-sequestrating cyanobacteria contribute substantially to global CO_2 reduction. The ocean hydrocarbon cycle includes the short- and long-term cycles related to the mitigation of petroleum hydrocarbons from natural seeps and anthropogenic oil spills, as well as the sequestration of CO_2 to produce oil reservoirs [160]. Two types of microbes, i.e., petroleum microbes and CO_2-sequestrating cyanobacteria, are crucial players participating in the cycles [161]. The short-term cycle occurs over a few days and starts from the CO_2 sequestration for producing O_2 and biomass via cyanobacterial photosynthesis. In contrast, the long-term cycle takes millions of years to convert marine organic matter to crude oil in sediments forming oil reservoirs via diagenesis and catagenesis. This ecologically inspired approach can be employed for carbon-neutral engineering applications: Promisingly, the CO_2 would be sufficiently decarbonized to O_2 to add to the metabolic process in petroleum microbes to enhance biodegradation and bioproduction. Regarding the harness of cyanobacteria, the marine cyanobacterial *Prochlorococcus* and *Synechococcus* participated in the ocean hydrocarbon cycle, accounting for about 25% of ocean primary production [162], are vital members of phytoplankton communities and could act as crucial models in this issue. However, *Prochlorococcus* prefers to distribute in warm regions, whilst *Synechococcus* distributes across latitudes from warm to cold areas. It implies the selection and screening of local *Synechococcus* species could enable CO_2 fixation in a broad range of temperatures, particularly tackling the challenging issue of biotic CO_2 capture in cold regions. Further, the genetic engineering and cultivation techniques of *Synechococcus* are also mature, and the produced biomass can be further harnessed to generate useful chemicals [163], suggesting the widely distributed, easily cultivated, and simply genetically manipulated *Synechococcus* might be employed as the candidate involved in the co-culture system for achieving carbon neutrality.

Bioreactor design

In industrial applications, the reactor-based approach offers an ideal environment with sufficient mass transfer and management of parameters (temperature, agitation, oxygen, maintenance of sterility, etc.) to stimulate microbial functions and activities. Typically, large-scale bioproduction is developed from step-forward bench-scale systems. After the rational microbial design, species should be first cultivated in the flasks to evaluate their performance, then used in a lab-scale fermentation reactor to test the engineering feasibility, and finally used for pilot-scale production.

It is challenging to realize the rational design of bioreactors for production and the optimization of complex operational parameters. Regarding the design of bioreactors, multiple types and modes have been reported, including stirred tank [164], bubble column bioreactor [165], fluid/packed bed fermenter [166], photobioreactor [167], membrane bioreactor [168], etc. The deployment of petroleum microbes can simplify the reactor system: (1) the control of temperature can be omitted by using cold-tolerance species; (2) the maintenance of sterility can be removed by using the high salinity; and (3) the oxygen supply can even be dropped by co-culture with cyanobacteria. In addition, the energy for agitation may be obtained from the natural ocean waves, which deserves future investigation. Furthermore, although the stated strategies can help save massive energy and steps for industrial operations, multiple complex parameters should be intelligently monitored and optimized. Beyond this, the muti-factor mediated design approach should be developed to control not only parameters in bioreactors but also the genetic and metabolic manipulation in the whole system, to completely realize the sustainable goals.

Conclusions

Climate change impacts on the marine industry raise challenges and demand better solutions. The development of petroleum microbiology provides promising solutions supporting sustainable developments under climate change conditions. In offshore oil and gas, microbial monitoring can provide a safe and rational understanding of the oil and gas reservoirs beyond the seismic survey; microbial-enhanced oil recovery and bioremediation of oily wastes, depending on the microbial capacity for the production of biosurfactants and degradation of hydrocarbons, are green pathways for oil recovery and pollution mitigation. To facilitate sustainable shipping, petroleum microbiology can support upgrading dirty oils (i.e., biodesulfurization, biodenitrogenation, and biodemetallization) and producing biofuels to replace traditional dirty HFO. In fishery, the capacity of petroleum microbes to degrade plastics and biorefining fishery wastes has been identified for the circular economy. These activities are largely beyond the conventionally known microbial biotechnologies in the oil and gas industry and advocate the new-era petroleum microbiology.

To further employ the new-era petroleum microbiology for benefiting our marine environment and responsible economic growth, we offer insights into the challenges and future research opportunities for the promotion of advanced microbial monitoring, the rational microbial design for enhanced product generation and carbon neutrality, and the sustainable bioreactor design. Since the petroleum microbes host many superiorities to the traditional model species, we believe multidisciplinary cooperation targeting new-era petroleum microbiology can lead to various technological breakthroughs to completely support the blue economy and benefit human society.

Data availability

The original data are available from the corresponding authors upon reasonable request.

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Author contributions

Y.C. did the literature review and wrote the manuscript. G.D. did the literature search and figure visualization. B.Z. and B.C. supervised the project and reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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