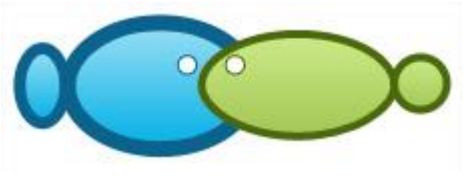

Plastic-degrading bacteria in deep-sea ecosystems: A review

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Abstract. Plastic pollution in marine ecosystems is increasing every day and causes many problems in various lines of life. Plastic that enters the sea surface will be exported to the deep-sea and to the seafloor sediments, where it accumulates. The plastic degradation process is one way to reduce its amount in the environment. The most promising is the biodegradation process in which microorganisms utilize plastic polymers as a carbon source and break them down into monomers. The search for potential bacterial strains to degrade plastics requires appropriate techniques. This is because the extreme deep-sea ecosystem demands the availability of various equipment for sampling, laboratory testing, and characterization of capabilities for plastic degrading. This process is important to obtain potential strain candidates capable of degrading plastic in extremely deep-sea ecosystems.
Key Words: deep-sea bacteria, extreme ecosystem, plastic degrading.

Introduction. The deep-sea provides extreme ecosystems for all the biota, including microorganisms (Liang et al 2021). The anthropogenic pressures on land, however, also influence both the abiotic and biotic components of this ecosystem (Machado et al 2018). Moreover, plastic pollution, which continues to increase every year, may impact the physical, chemical and biological structures of the environment (Li et al 2021). The investigation of deep-sea bacteria has gained considerable attention, owing to the enormous potential in the field of biotechnology, including as bioremediation agents (Tomasino et al 2021). The studies on the biodegradation of plastics by deep-sea bacteria are still limited (Atanasova et al 2021) due to various challenges in the isolation, identification, and characterization of deep-sea bacteria. This paper will discuss the potential of the deep-sea bacteria in plastic degradation, including the degradation mechanism, as well as the isolation technique and characterization of the deep-sea bacteria. Handling plastic pollution in the ocean is expected to be reduced by the use of bacteria adapted to extreme environments in the biodegradation process.

Extreme deep-sea ecosystems. The deep-sea can be defined as the sea at the depth of 200 m, where solar energy is not able to support the productivity of the primary photosynthesis. The data shows that 50% of the oceans are below 3,000 m deep, with an average depth of 3,800 m (Tyler et al 2016). The deep seafloor, which has long been considered a stable environment, has been reported to support one of the highest biodiversity on the planet in a wide variety of interconnected habitats (Tyler 2003). The ecosystem diversity gives a great influence on the distribution and diversity of macro and micro-organisms in which biotic and abstract components interact. Although the deep sea covers more than 60% of the earth's surface, less than 1% of the area has been scientifically investigated. Despite the scientific knowledge has been substantially improved in recent decades, there are large gaps in the coverage of global sampling from the deep sea, and great efforts are continuously directed towards offshore research (Tyler et al 2016).

The research related to biodiversity resources is currently focused on the sea, which is still less explored than the land resources. The extreme deep-sea ecosystems can be characterized by their high or low temperatures, low pH, high salt concentrations, and high pressure, where the variety of biodiversity is still largely undisclosed. According to their ecosystems, the microorganisms in the extreme deep-sea ecosystems can be classified into thermophile (high temperature), psychrophile (low temperature), halophile (high ionic strength), alkalophile/acidophile (acidic or alkaline pH value), piezophile (high pressure), and polyextremophile (Poli et al 2017). Additionally, the deep-sea ecosystems have hydrothermal vents which provide the energy/nutrient flow required to support the diverse microbial communities scattered across the temperature range, and the decrease in compound gradient is correlated with the transition from oxic to anoxic conditions (Canganella 2001). In the deep-sea hydrothermal ventilation system, there is an environmental gradient that eventually produces many ecological niches, leading to the diversity of the microorganism community (Fang et al 2010; Kato et al 2008). Microorganisms in this ecosystem are extensively being studied since they have great prospects in the development of biotechnology. Marine microorganisms are a rich source of structurally and biologically active new metabolites. Studies on deep-sea microorganisms have been focused on their ability in the biogeochemical process, bioremediation of pollution, and the production of bioactive compounds as new drugs (Donato et al 2018).

Plastics in the deep sea. The vastness of the ocean on earth requires it to provide important resources including, food, energy, and water. Therefore, the changes in marine ecosystems caused by anthropogenic stress, such as plastic pollution, can have global dramatic impacts on the deep sea. There are about 100 million tons of plastics used in various industrial sectors in the world every year. The main sources of synthetic plastic waste in the marine environment originate from coastal tourism, fisheries, the marine industry, and the manufacture of plastic products that have a direct impact on the oceans (Cole et al 2011). The average use of plastics in Asia is up to 20 kg per year per person and is expected to continue to increase. Compared to other continents, Asia consumes about 30% of the world's plastic, followed by America, Europe, and other continents. Indonesia, with a large population and an extensive coastline, is in the second rank as the largest contributor to plastic waste in the world (Jambeck et al 2015; Lebreton et al 2017).

Five to thirteen million tonnes of plastic waste is estimated to enter the oceans each year (Jambeck et al 2015; Lebreton et al 2017), but only a few hundred thousand tonnes are reported to enter the ocean surface (Eriksen et al 2014; Lebreton et al 2018). This is due to various processes, such as the continuous export of plastics from the surface to the seafloor and the fragmentation of plastic waste into countless micro or nano-plastic particles (Eriksen et al 2014). Depending on their density, plastics may accumulate in the water column of the central convergence zone and may either float on the surface (Cózar et al 2014; Pauli et al 2017) or sink to the seafloor after being filled with biotic and abiotic dissolved compounds (Bergmann & Klages 2012; Derraik 2002).

The ability of plastics to float on the surface of the water is due to the presence of acrylic components and other components that have high buoyancy and hydrophobicity (Andrady 2011; Woodall et al 2014). In addition, the plastic components, such as polyethylene and polypropylene also cause most plastics to have a lower density compared to seawater and lead the plastic to float on the sea surface (Andrady 2011). However, due to various processes in the oceans, plastic can sink due to particle adhesion and biofouling, resulting in the accumulation of the plastic on the seafloor (Woodall et al 2014). The data shows that the accumulation of plastics at the ocean surface is only 1% of the estimated amount of global plastic waste in the ocean, of which 99% ends up in the deep sea (Lebreton et al 2017; Gewert et al 2015; Eriksen et al 2014; Woodall et al 2014; Andrady 2011). Most of the plastic pieces in the deep sea are in the form of small fragments of microplastics (<1 mm) and fibers (Lobelle & Cunliffle 2011) which come from the production of synthetic textiles (Gijsman et al 1999) or from the fragmentation of larger plastic waste (Yousif et al 2012).

Petrochemical plastics, such as polyvinyl chloride (PVC), polyethylene (PE), polypropylene (PP), polystyrene (PS), and polyethylene terephthalate (PET) (Figure 1) contribute with up to 80% to the total global plastic usage.

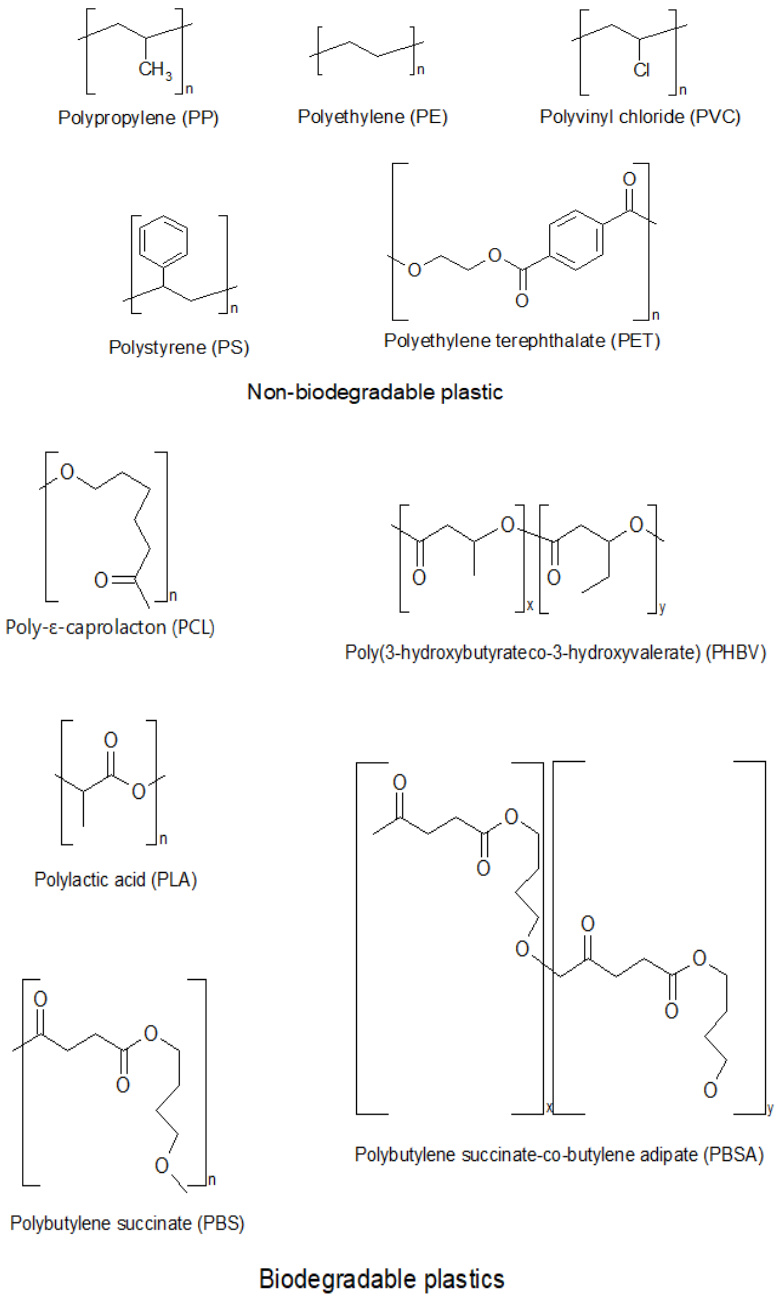

Figure 1. Structures of non-biodegradable and biodegradable plastics.

Polyethylene (PE) is a widely used synthetic polymer due to its lightweight, inexpensive, strong, and durable properties. The production rate for synthetic polymers is nearly 140 million tons (Sekhar et al 2016) and approximately 500 billion to 1 trillion bags of Low-Density Polyethylene (LDPE) are consumed annually worldwide. Furthermore, PE has strong C-H and C-C bonds which make it resistant to natural degradation and lead to accumulation in the environment. As a consequence, their disposal poses major ecological problems and is one of the main sources of pollution (Kyaw et al 2012). The current studies are directed to the development of biodegradable plastics (Figure 1) such as poly-ε-caprolactone (PCL), polylactic acid (PLA), polybutylene succinate (PBS), polybutylene succinate-co-butylene adipate (PBSA) (Tokiwa & Calabia 2004), and poly(3-

hydroxybutyrateco-3-hydroxyvalerate) (PHBV) (Urbanek et al 2018). However, these efforts are not yet able to prevent the abundant pollution due to plastic waste.

The ability of the deep-sea bacteria for plastic degradation. The adverse effects of plastic pollution on marine ecosystems and human health are of a great concern, but the amount of plastic entering the sea continues to increase every year (Lebreton et al 2018; Thompson et al 2004; Eriksen et al 2014). Therefore, considerable efforts to improve the degradation process are carried out. The degradation of the ocean plastic waste into microplastics and nanoplastics previously described is influenced by abiotic and biotic factors (Pauli et al 2017). The perfect degradation process should convert the polymer into organic acids, CO_2, CH_4, and H_2O (Zitko & Hanlon 1991). Degradation of plastic waste initially occurs through the abiotic photo-oxidation when exposed to UV light (Mason et al 2016; Thompson et al 2004) followed by polymer cleavage (Browne et al 2011). However, many plastic polymers are resistant to photo-oxidative processes, including PP and PE (Andrady 2011). Physical and chemical degradation can also occur in the oceans in the form of passive hydrolysis; the process is, however, very slow and does not apply to certain types of polymers (Ballent et al 2012; Thompson et al 2004). In addition, both methods are expensive and produce toxic waste which can also pollute the environment. Biodegradation by microorganisms has been considered an environmentally friendly method to degrade plastics. In this context, the polymers are utilized as the carbon sources by microorganisms. Microorganisms produce the extracellular enzymes that may cleave the polymer chains into small monomers/oligomers, which in turn undergo the metabolism process into water and carbon dioxide (Ojha et al 2017). Several factors are related to the plastic degradation process by marine microorganisms, including the ability of bacteria to form biofilms and environmental factors. The ability of bacteria to form biofilms is influenced by the surface structure of topography, electrostatic interactions, roughness, free energy, and hydrophobicity (Rummel et al 2017), and material properties. On the other hand, the environmental factors that influence the degradation process are oxygen levels, salinity, light opacity, and temperature (Dash et al 2013; De Tender et al 2015).

To date, there have been only very few reports on plastic-degrading bacteria in the deep sea. However, several studies have demonstrated the ability of deep-sea bacteria to degrade plastics (Table 1).

Table 1

Plastic-degrading bacteria in the extreme deep-sea ecosystems

Plastic	*Bacteria*	*Source*	*Depth*	*Reference*
PCL	*Pseudomonas* sp.	The deep-sea at Tottori Prefecture	2,000 m	Sekiguchi et al 2009
PCL	*Shewanella*, *Moritella* sp., *Psychrobacter* sp., *Pseudomonas* sp.	The deep-sea sediment at Kurile and Japanese Trenches	5,000-7,000 m	Sekiguchi et al 2010
PCL, PHB/V, PBS	*Pseudomonas* sp., *Alcanivorax* sp., *Tenacibaculum* sp.	Deep-sea water	320-650 m	Sekiguchi et al 2011
PS	*Bacillus paralicheniformis*	The deep-sea sediment at Arabian Sea	3,538 m	Kumar et al 2021

Sekiguchi et al (2010) reported the interaction of plastic-degrading bacteria with the extreme deep-sea ecosystems, low temperature, and high pressure. Two types of PCL-degrading bacteria were isolated from the deep-sea water at the depth of 320 m in Toyama Bay. The isolated strains were identified as the genus *Pseudomonas* and were

able to degrade PCL at 4°C (Sekiguchi et al 2009). In addition, bacteria from the genera of *Shewanella*, *Moritella*, *Psychrobacter* and *Pseudomonas* were isolated from the deep-sea sediment samples at the depth of 5,000–7,000 m. Six bacterial strains showed degradation activity against the biodegradable PCL polyester. This group also evaluated other biodegradable plastics such as PLA, PBSA, PBS, and polyhydroxybutyrate (PHB), but no activity was observed (Sekiguchi et al 2010). However, in the following report, it was stated that PCL, PHB, and PBS fibers could be degraded in the deep sea even though the temperature was low. Furthermore, five PCL-degrading strains isolated from deep water (320-650 m depth), were identified bacteria from the genera of *Pseudomonas*, *Alcanivorax*, and *Tenacibaculum*. Two of them, *Pseudomonas* spp. strains RCL01 and TCL04 were found to adapt to conditions of low temperature (4°C) and high hydrostatic pressure (Sekiguchi et al 2011). However, the problems of isolation, identification, and characterization of deep-sea bacteria are still to be addressed. Ravenschlag et al (1999) reported that most of the 16S rRNA sequences of bacteria were not known to be associated with the existing isolates.

In the biodegradation process, the diversity of aliphatic polyester-degrading microorganisms is the most important factor in the degradation process. The biodegradation of complex polymers by bacteria occurred through several stages, including biodeterioration, depolymerization, assimilation, and mineralization (Pramilla & Ramesh 2015). The biodegradation of plastics due to the activity of certain enzymes gives rise to the breakdown of polymer chains into monomers and oligomers. The enzymatically degraded plastics are then absorbed by the microbial cells to be further metabolized. The aerobic damage produces carbon dioxide and water.

The involvement of enzymes in the microbial biodegradation of PE has been investigated. For instance, enzymes of lacases and esterases have been confirmed to either directly or indirectly play a role in the degradation process (Lucas et al 2008). The production of the laccase enzyme in the presence of PE as the only carbon source indicates that laccase plays a role in the degradation of the intermediate products generated during this process. Other enzymes, such as alkane hydroxylase, are also reported to be involved in the degradation of plastics by microorganisms (Sowmya et al 2014; Yoon et al 2012; Fujisawa et al 2001).

The saturated alkanes with C-12 to C-18 chains or longer are susceptible to be degraded by a wide variety of bacteria. On the other hand, the degradation of water-soluble short-chain alkanes such as pentane, hexane, heptane, and octane is less frequent due to their toxicity to the environment (Tani et al 2001; Bouchez-Naitali et al 1999; Leahy & Cowell 1990). The degradation pathway for *n*-alkanes has been extensively studied in *Pseudomonas putida* GPo1 (van Beilen et al 1994). The related information concerning the marine bacteria has not been found. The conversion of *n*-alkanes of C5-C12 to fatty acids in this strain was mapped to a large plasmid, the OCT plasmid. The first step of the alkane degradation is the oxidation of the methyl groups to alcohol by the "alkane hydroxylase system" which consists of a membrane-bound monooxygenase, alkane hydroxylase per se (45.8 kDa), encoded by alkB, and an electron transport system solution consisting of two rubredoxins and an NADH-dependent-reductase rubredoxin, which are encoded by alkG, alkF, and alkT. The specific oligonucleotide primers for the GPo1 alkB gene have been used for PCR amplification to analyze alkane biodegrade populations in various environments (Vomberg & Klinner 2000; Whyte et al 1996). The alkB-related sequences are mostly found in Gram-negative bacteria which grow with the short-chain n-alkanes. Smits et al (1999) employed the degenerating oligonucleotide primers to amplify the alkB/alkM-related sequences of a series of bacteria including strains of *Pseudomonas*, *Acinetobacter* and *Rhodococcus*.

Deep-sea bacteria isolation and characterization approaches for plastic degrading. The discovery of potential bacterial isolates in solving the problem of plastic waste requires proper isolation and characterization techniques. The studies on the isolation of deep-sea microorganisms are costly since the expeditions require research vessels. The deep-sea samples which are usually used to investigate the diversity and biological potential of microorganisms consist of seawater, seafloor sediments, and deep-

sea biota. The sampling of seawater at a certain depth utilizes the oceanographic instrument in the form of a Conductivity Temperature Depth (CTD) equipped with a Niskin bottle that can collect water at different depths (Suter et al 2016). Meanwhile, for samples of unconsolidated sediment and organisms on the seafloor, a grab and box corer is used (Przeslawski et al 2018).

The characterization of marine bacteria can be carried out by either dependent or independent culture methods. While the former allows us to obtain the bacterial isolates by growing them on a certain medium and studying their biological potential, the latter is carried out by isolating the environmental DNA from both water and marine sediment samples and then isolating potential genes according to the required objectives. The latter method is also often known as metagenomics. The previous study demonstrated that the metagenomic studies of marine extremophile microorganisms give various new genes that can be used as sources of bioproducts such as enzymes and other metabolites. Further investigation of metagenomic studies is important to reveal the ecological, biochemical, and industrial potential of deep-sea microbes (Russo et al 2010; Trincone 2010).

One of the challenges is the isolation of the deep-sea bacteria in maintaining the isolation conditions, such as temperature and pressure, as in the extreme conditions in the deep sea. The use of a low-temperature room is one solution. Meanwhile, the isolation of piezophile bacteria can be carried out by using the high-pressure continuous cultivation using the DEEPBATH system described in Sekiguchi et al (2010). The isolates obtained are tested for their ability to degrade plastics by inoculation into a minimal mineral medium with the addition of plastic polymers as carbon sources. Furthermore, the ability of bacteria to degrade plastic into films is evaluated using FTIR and SEM. The Infra-Red (IR) spectroscopy is the analytical technique used in many biodegradation studies, i.e., by determining the formation or loss of functional groups. Therefore, the degradation products, the chemical groups incorporated into polymer molecules such as branches, co-monomers, the unsaturation, and the presence of additives such as antioxidants can be determined by this technique (Drimal et al 2007; Arboleda et al 2004; Kiatkamjornwong et al 1999; Klrbas et al 1999). The changes in the structure of the plastic film after UV irradiation and subsequent incubation with bacteria can be analyzed using the FTIR spectrophotometer. Technically, each sample is analyzed at the spectrum range of 4,000-650 cm^{-1}. The carbonyl index (CI) is determined to measure the degree of biodegradation and is calculated as the ratio of the maximum absorbance of the carbonyl group at 1,712 cm^{-1} versus the maximum absorbance of the CH_2 (methylene) group at 1,462 cm^{-1} (Hadad et al 2005). The equation used to calculate CI is expressed as (Hadad et al 2005):

$$\text{Carbonyl Index (CI)} = \frac{\text{Absorption at 1,712 } cm^{-1} \textit{ (the maximum of carbonyl peak)}}{\text{Absorption at 1,462 } cm^{-1} \textit{ (the maximum of carbonyl peak)}}$$

For the characterization of polymers surface using the Scanning Electron Microscope (SEM), the samples are air-dried, coated with platinum, and then exposed to SEM to determine the changes in plastic's morphology and the potential for bacterial biofilm formation (Cangemi et al 2006). The films are analyzed to identify any changes in surface morphology (pinholes, cracks, and holes) after being inoculated with plastic-degrading bacteria. Changes in morphological structure indicate the degradation of plastic polymers into simple monomers. The search for potential bacteria as plastic bioremediation agents with proper testing is expected to make a positive contribution to solving the problem of pollution in marine ecosystems.

Conclusions. The problem of increasing marine pollution with plastic requires a solution. One of the most effective steps is the use of microorganisms for degrading plastic through processes that are not harmful to the environment. Deep-sea ecosystems provide various microorganisms that can be utilized in biotechnology, including for the bioremediation of plastic waste. The processes of isolation and characterization of

potential bacteria, if properly carried out, could improve their plastic degradation abilities, contributing to solve the plastic pollution issue affecting the marine ecosystems.

Acknowledgements. The authors would like to thank the LIPI COREMAP-CTI 2021–2022 (17/A/DK/2021) for funding the processing charges.

Conflict of interest. The authors declare no conflict of interest.

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Received: 20 April 2022. Accepted: 11 June 2022. Published online: 25 June 2022.
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How to cite this article:
de Fretes C. E., Sohilait M. R., 2022 Plastic-degrading bacteria in deep-sea ecosystems: A review. AACL Bioflux 15(3):1531-1540.