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Review

Polymer material biodegradation in the deep sea. A review

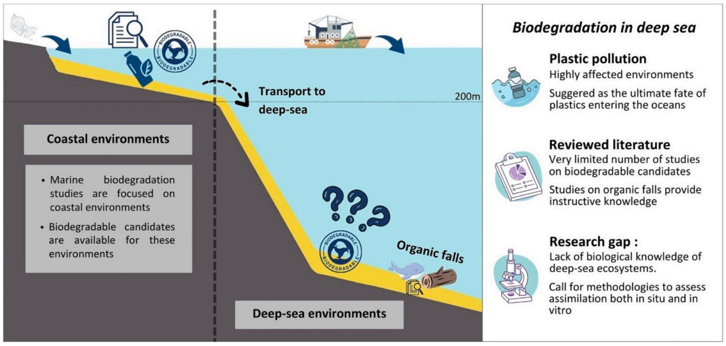
Alexandre Chamley [a,b,c,*], Christophe Baley [a], Marjolaine Matabos [d], Pauline Vannier [e], Pierre Marie Sarradin [d], Floriane Freyermouth [b], Peter Davies [c]

[a] Université Bretagne-Sud, IRDL, CNRS UMR 6027, BP 92116, Lorient Cedex 56321, France
[b] Thales DMS, Brest, France
[c] Ifremer RDT, Research and Technology Development Unit, Plouzané 29280, France
[d] University Brest, CNRS, Ifremer, UMR 6197 Biologie Et Ecologie Des Ecosystèmes Marins Profonds, Plouzané 29280, France
[e] Laboratoire MAPIEM, E.A.4323, Université de Toulon, CS 60584, 83041 Cedex 9 Toulon, France

HIGHLIGHTS

- Deep-sea biodegradation studies are crucial to develop sustainable marine materials.
- The literature is extremely limited on the subject.
- Studies conducted on organic falls provide instructive insights.
- The technical and methodological gaps preventing generic conclusions are discussed.

GRAPHICAL ABSTRACT



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ABSTRACT

The phenomenon of marine plastic pollution is now well-established, with documented impacts on marine biodiversity and biogeochemical cycles. In order to mitigate this environmental impact, a significant amount of research has been conducted in recent years with the objective of developing biodegradable alternatives to conventional polymers and their composites in marine environments. The findings of this research significantly enhanced our understanding of biodegradation mechanisms and identified promising candidates. However, the majority of these studies have been conducted in coastal marine environments, which represent a minor component of the marine ecosystem. Recent models on the transport of plastic debris in the oceans indicate that deep-sea environments are likely to be the ultimate sink for a significant proportion of plastics entering the oceans. The aim of this review is to provide an overview of the processes of biodegradation of polymers in these deep-sea environments. The diversity and specific characteristics of these environments with respect to degradation mechanisms are discussed. While the majority of deep-sea conditions are not conducive to biodegradation, studies on organic falls (wood and whale carcasses) and a few investigations into materials previously shown to be biodegradable in coastal marine environments demonstrate mechanisms that are similar to those observed in shallow waters. Nevertheless, further research is necessary to reach definitive conclusions. It is essential to extend these studies to a broader range of deep-sea environments. Additionally, new methodologies that

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* Corresponding author at: Thales DMS, Brest, France.
E-mail address: alexandre.chamley@thalesgroup.com (A. Chamley).

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integrate microbiology and polymer science are required to accurately assess the process of assimilation of these materials in these environments.

1. Introduction

1.1. Plastics pollution in the oceans

The use of plastic materials on a global scale started in the 1960s. Since then, the production of these materials has steadily increased and reached 390 million tonnes in 2021 (Plastics Europe, 2022). They are employed for a very wide range of applications, from construction to packaging and clothing. This systemic consumption has led to global pollution, that is one of the major issues of our time (Persson et al., 2022; United Nations Environment Assembly, 2022).

Since the 1970s and the first reviews that outlined the harmful effects on the marine fauna (Coleman and Wehle, 1984; Laist, 1987), the scientific community has worked to characterise this pollution and its impact on the Earth's ecosystems, particularly marine. Models of the accumulation of plastic waste in the ocean and in-situ studies show that all marine environments are affected: the surface (Eriksen et al., 2014), the water column (Galgani et al., 2022; Harris et al., 2023; Pabortsava and Lampitt, 2020) and the deep sea (Harris, 2020; Woodall et al., 2014). This has resulted in multiple negative effects on the marine flora and fauna. Macroplastic debris causes entanglement and suffocation via ingestion (Laist, 1987). Micro- and nanoplastics absorb and transport chemicals that are toxic to marine life when ingested (Everaert et al., 2018; Hermabessiere et al., 2017; Thushari and Senevirathna, 2020). Cocktail effects make experimentation difficult and may cause an underestimation of the risk for living creatures. This contamination affects the entire marine food chain with consequences for the marine ecosystem and ecosystem services (Thushari and Senevirathna, 2020; Worm et al., 2017).

Most studies on plastic pollution in marine ecosystems refer to either littoral or epipelagic ecosystems. However, recent studies and reviews have raised concerns about the potential threat of plastic litter pollution in the deep sea. Macroplastics have been observed in various deep-sea environments (Angiolillo et al., 2021; Grøsvik et al., 2023; Hernandez et al., 2022; Nakajima et al., 2021), including the deepest marine trenches (Abel et al., 2023). High concentrations of microplastics in sediments have also been observed in a wide variety of environments, depths, and locations (Abel et al., 2023; Cunningham et al., 2020; Feng et al., 2023; Pinheiro et al., 2023; Tsuchiya et al., 2024; Zhang et al., 2020). And recent modelling studies suggest that the deep sea may be the ultimate fate of a significant proportion of plastics entering marine environments (Harris et al., 2023; Woodall et al., 2014) (Fig. 1). A proportion of low-density plastics in the epipelagic zone is likely to sink as a result of flocculation and subsequent colonisation by microorganisms and algae (Li et al., 2023) and high density plastics are predicted to be remobilised and transported by bottom currents from coastal environments to abyssal and hadal zones (Kane et al., 2020; Pohl et al., 2020). Although the impact of micro and macro plastics on deep-sea fauna is not yet well understood, initial studies have yielded similar conclusions to those conducted on the surface. Macro debris causes entanglement (Angiolillo et al., 2021) and modifies habitat characteristics (Jamieson and Onda, 2022). Fauna contamination by microplastics and glass fibres has been observed (Ciocan et al., 2024; Jamieson et al., 2019; Muthu et al., 2023; Taylor et al., 2016; Zhang et al., 2020) and toxic effects have been characterised (Everaert et al., 2018; Haegerbaeumer et al., 2019; Muthu et al., 2023).

1.2. Marine biodegradation

To tackle this major pollution issue, our societies have several levers for action (UN Environmental programme, 2019). In cases where loss at sea is unavoidable, one solution is to substitute plastic materials by polymers that are biodegradable in the deep-sea environments (Narancic and O'Connor, 2019; Shen et al., 2020).

Biodegradation is a complex process that involves a series of successive and/or concomitant mechanisms that facilitate the breakdown of

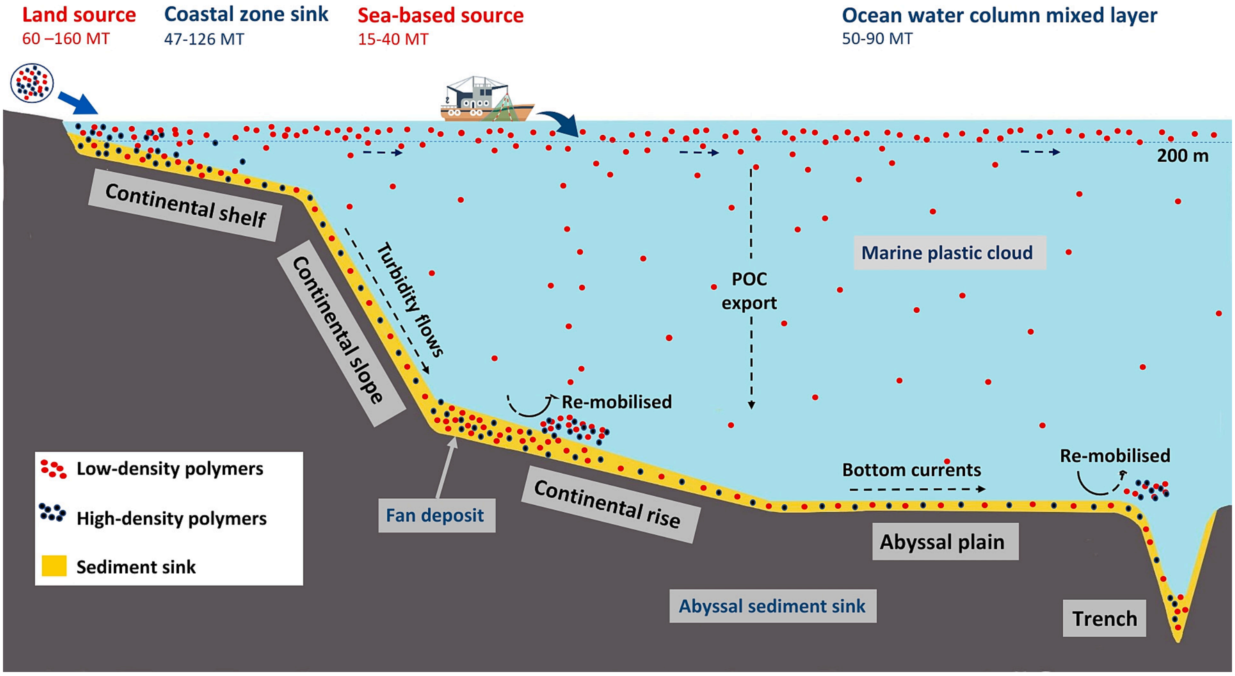

Fig. 1. The fate of plastics litter in marine environments.
Adapted from Harris et al. (2023).

biodegradable matter until it is assimilated by living organisms. The constituent elements of this material then reintegrate their natural cycles, such as carbon in wood. For polymer materials, this process is composed of three main mechanisms: deterioration, molecular fragmentation, and assimilation (Fig. 2). Biodegradation of polymers has been extensively studied by the scientific community, and the three mechanisms mentioned above are well defined in the literature. Main details can be found in the following reviews (Laycock et al., 2017; Lucas et al., 2008; Wang et al., 2021).

These mechanisms are impacted by many factors that can be classified in two categories: biotic and abiotic. Deterioration is the process of matter decohesion at a macromolecular scale, primarily caused by the rupture of hydrogen bonds. It is mainly affected by abiotic factors (e.g. mechanical stresses, photodegradation). Molecular fragmentation involves the cleavage of carbon chains usually by hydrolysis or oxidation depending on environmental conditions and the nature of the polymer. Carbon chain breakage can be catalyzed by extracellular enzymes secreted by microorganisms present in the degradation environment (i.e., biofilm in marine environments), a process referred to as biofragmentation. The degradation rates resulting from biofragmentation can be up to ten times faster than abiotic molecular fragmentation, depending on the environment, particularly its temperature, and the presence of microorganisms capable of secreting these enzymes, which is often the limiting factor in the biodegradation process (Laycock et al., 2017). Assimilation is the ultimate stage of the biodegradation of a material. It occurs through the mineralisation of oligomers from the preceding stages of degradation by microorganisms. Therefore it depends on the bacterial communities present in the biofilm that colonize the degraded material and consequently on the bacterial community present in the degradation environment (Albright and Chai, 2021; Harrison et al., 2018; Pires et al., 2022).

Drawing general conclusions about polymer biodegradation in marine environments is currently challenging due to the relatively recent field of study and materials considered. Results obtained so far are highly variable because of the wide variety of conditions encountered in marine environments and the difficulty in establishing laboratory tests representative of field conditions (Chen, 2022; Haider et al., 2019), leading to important knowledge gaps (Harrison et al., 2018; Wang et al., 2021). To assess marine biodegradability of a material there is currently no certification standard, unlike other degradation conditions such as industrial composting (ASTM D6400–23 (ASTM, 2023), ISO 17088:2021(ISO, 2021a)). International bodies have proposed standard laboratory tests for several conditions such as ISO 18830:2017 (ISO, 2017) and 19,679:2020 (ISO, 2020), or ASTM D6691–17 (ASTM, 2017), along with a standard for in-situ tests (ISO 22766:2021 (ISO, 2021b)). However, these documents have been the subject of criticism from the scientific community (Albright and Chai, 2021; Haider et al., 2019; Harrison et al., 2018; Van Rossum, 2021; Wang et al., 2021). (i) The standards are not sufficiently restrictive concerning the micro-organisms to be used (Haider et al., 2019; Harrison et al., 2018) (ii) The environmental conditions used in experiments are not representative of real conditions (high nutriment concentrations, temperature and/or oxygen content), leading to potential critical overestimations (Van Rossum, 2021). (iii) Materials are studied in powdered form, which overlooks scale effects and the deterioration stage. Recent studies have attempted to address these criticisms, particularly by combining tests under real conditions with laboratory tests (Briassoulis et al., 2024, 2020; Jacquin et al., 2021; Lott et al., 2021, 2020; Royer et al., 2023) and by selecting the micro-organisms via an initial biofouling stage in real environments (Cheng et al., 2022; Jacquin et al., 2021). While the aforementioned tests may potentially overestimate the biodegradation of a material and should be considered with caution, their results together with environmental studies have allowed a first discrimination of the materials to be considered for marine biodegradation.

The most promising materials include the polyhydroxyalkanoates (PHAs) specifically the short-chain PHAs such as poly(3-hydroxybutyrate) (P3HB) and its *co*polymer poly(3-hydroxybutyrate-co-3-hydroxyvalerate) (PHBV), polycaprolactone (PCL), and regenerated cellulose. Several studies have reported the biodegradation of these materials in marine environments (Briassoulis et al., 2020; Cheng et al., 2022; Deroiné et al., 2015; Kwon et al., 2023; Lott et al., 2021; Royer et al., 2023, 2021). In contrast, the most developed biopolymers, including polylactides (PLA), poly(butylene adipate terephthalate) (PBAT) or polybutylene succinate (PBS), have demonstrated negative

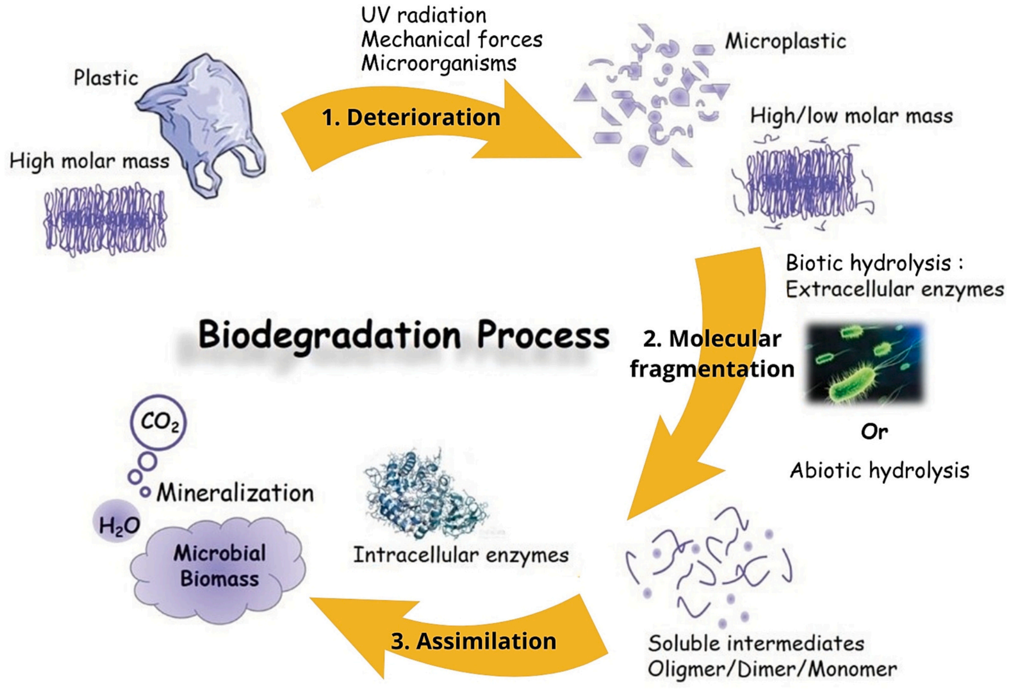

Fig. 2. Degradation mechanisms of biodegradation process.
Adapted from Wang et al. (2021).

results in these environments (Harrison et al., 2018). Polylactides, which can be composted on industrial compost, show no signs of biodegradation (and minimal degradation) after several months in natural marine environments (Deroiné et al., 2014a; Royer et al., 2023) and, to our knowledge, assimilation has never been reported in laboratory tests (Cheng et al., 2022; Jacquin et al., 2021). PBAT and PBS show signs of biodegradation in specific marine environments conducive to degradation, such as coastal environments and ports, close to human activities (Jacquin et al., 2021; Kwon et al., 2023; Nagamine et al., 2022). However, their degradation kinetics are relatively slow compared to the aforementioned candidates (PHAs, Cellulose), and they have been reported to remain intact in more remote environments (Nakayama et al., 2019; Omura et al., 2024; Sekiguchi et al., 2011a). These results emphasize the need to consider the specific environment in which the studied material will be released when assessing its potential biodegradability. In order to cover a wider range of mechanical properties, some studies investigate the biodegradation of their bio composites, using natural fibres for reinforcement (Meereboer et al., 2020; Rajeshkumar et al., 2023). Again only a few studies have been performed, first results indicate that the biodegradation of a composite is contingent upon the matrix's ability to biodegrade in that environment and that the reinforcement with natural lignocellulosic fibres enhanced the biodegradation processes and especially the bio deterioration (Meereboer et al., 2021; Rajeshkumar et al., 2023; Read et al., 2024; Seggiani et al., 2018).

1.3. Deep-sea biodegradation

Concerning deep-sea environments, the state of knowledge on biodegradation is very limited. Only a very limited number of studies have been performed and the aforementioned methodological issues present even greater challenges in these environments. This review aims to introduce the specificity of deep-sea environments with regard to biodegradation processes and to identify the numerous knowledge gaps that the scientific community should address to allow the development of biopolymers and biocomposites with truly biodegradable properties in deep-sea environments. Firstly, the diversity of these environments and the multiple factors that could affect the biodegradation processes are described. Then the limited examples of studies on material biodegradation that have been characterised in these environments are reviewed. And finally the available methods to evaluate the biodegradability of alternative polymers both in situ and in the laboratory are discussed.

2. The deep ocean

The deep ocean remains today among the least known environments geographically, biologically and geophysically (Danovaro et al., 2014). Its exploration started in 1872–76 with the Challenger expedition, which discovered deep sea fauna (Murray, 1895). But it was in the 1960's, with the development of deep-sea scientific vehicles (Remote operational vehicles ROV), that more extensive studies became possible. Since then technical innovations have made deep-sea investigations more accessible with the installation of the first observatories which enable regular sampling (Favali and Beranzoli, 2009). This section will provide a short overview of the environments included in the deep ocean with specific focus on the principal factors that could potentially influence the biodegradation of materials that ultimately reach this environment.

2.1. Deep-sea environments

The deep ocean is defined as the regions below 200 m depth and includes a large number of different environments (Harris et al., 2014; Ramirez-Llodra, 2020), see Fig. 3. It begins where the continental shelf ends and is usually divided into three distinct areas: the continental slope, the abyss and the hadal zone (Harris et al., 2014). A number of geological features account for the large diversity of landscapes and ecosystems that characterise these three zones (Harris et al., 2014). They include abyssal plains, hills and mountains, continental slopes, continental rises, submarine canyons, mid-ocean ridges, trenches and troughs, seamounts, to cite only the major features (Fig. 3). Each of these subdivisions has its own specific types of biological community from micro- to macro-fauna, some of which can be endemic to a given ecosystem, and differences within taxonomic groups have been observed between different deep-sea environments (Harris and Baker, 2020; Ramirez-Llodra et al., 2010). Furthermore although the ocean is one volume and all regions are interconnected, species also vary depending on ocean basins and along geographical gradients for a given ecosystem (Moalic et al., 2012; Thompson et al., 2024; Tyler et al., 2002). Therefore, a biodegradable waste item reaching the deep-sea environments may encounter a multitude of diverse living communities depending on the specific region in which it is located.

Deep-sea environments represent a substantial proportion of the ocean floor, encompassing 91 % of the total oceanic area (Harris et al., 2014). Of these environments, abyssal zones are the most extensive, covering 84.7 % of the ocean surface, followed by the continental slope

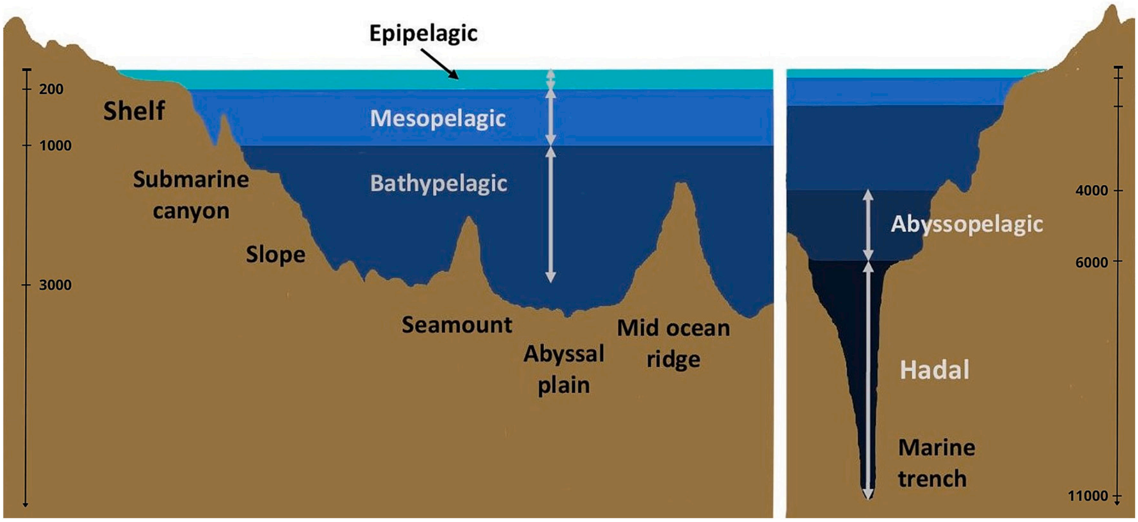

Fig. 3. Deep-sea environments.
Adapted from Ramirez-Llodra (2020).

(5.42 %), and the hadal environments (less than 1 % of this area).

Abyssal zones include various ecosystems, primarily abyssal hills (41 % of the total seafloor area), abyssal plains (28 %), and abyssal mountains (16 %). These three ecosystems are the most prevalent in the deep sea and are characterised by their distinctive topographies, which are influenced by the underlying basalt layer and cause significant heterogeneity in quantity of nutrients, biomass and biodiversity (Morris et al., 2016). They are mostly oligotrophic and subjected to highly stable environmental conditions: high hydrostatic pressures (≈ 1 bar for each 10 m depth), low temperatures (≈ 2 °C), slow bottom-currents and relatively low but stable levels of dissolved oxygen (≈ 5–6 ml L^{-1}) (Ramirez-Llodra et al., 2010). They support a very high biodiversity and low biomass, mainly composed of micro and meiofaunal organisms (Ramirez-Llodra, 2020). These organisms, heterotrophic, feed on organic matter from the epipelagic zones and from the continent, brought by gravity and lateral currents respectively (detailed below). The abyssal zones comprise other environments including mid ocean ridges or seamounts that are biologically unique but not directly relevant for this review as they represent respectively 0.2 % and 2 % of the seafloor surface, more information can be found in the following references (Dick, 2019; Levin et al., 2016; Rogers, 2018; Rowden et al., 2010).

The continental slopes extend from the shelf break on the landward side to the abyss zone on the seaward. They cover 5.2 % of the ocean surface (Harris et al., 2014) and are usually delimitated seaward by a continental rise or trenches/troughs depending on the nature of the margin (passive or active). They are characterised by an important slope angle, means of 3.8 and 6 degrees respectively for passive and active margins, and a layer of sediment that is also dependent on the margin type (thick for passive margins and thin for active). Continental slopes also encompass different habitats including submarine canyons, cold seeps (i.e. sources of methane and H_2S), mud volcanoes and terraces that are hotspots of benthic and pelagic biota (Fernandez-Arcaya et al., 2017; Levin et al., 2010; Menot et al., 2010). These environments exhibit high heterogeneity of geochemical conditions with relatively low pressure, high temperature and important concentrations of nutrients coming from the continent landward and high pressure, low temperature and a lower concentration of nutrients seaward (Levin and Sibuet, 2012). This heterogeneity causes significant shifts in organisms present in these environments along the slopes and generates and maintains a high biomass and biodiversity. These environments are also subject to influence from currents originating from the continental shelf situated landward, which result in the transport of nutrients (and plastic litter) towards abyssal zones. Despite representing a relatively minor portion of the ocean floor, these environments are likely to be pathways for the transport of plastic litter into abyssal regions (Harris et al., 2023) and, as a result, should be considered as potential degradation environments for plastic waste.

Hadal environments are rarer and occupy only 1 % of the seafloor, they are composed of deep trenches and troughs mainly located near active margins. To date 46 deep trenches have been identified (33 trenches and 13 troughs) (Jamieson, 2015). The environmental conditions in these environments are comparable to those of the abyssal plains, with temperatures ranging from 1 to 4 °C and a salinity level of approximately 35 %. However, oxygen content in these environments shows large variability as a consequence of the influence of significant bottom currents and high respiration rate resulting from significant organic matter deposition. Furthermore, they are subjected to extreme hydrostatic pressure, with values ranging from 600 to 1100 bars (Jamieson, 2015). These conditions result in the presence of highly specific fauna that is specifically adapted to these regions (Blankenship-Williams and Levin, 2009; Liu et al., 2018; Pradillon and Gaill, 2007). The majority of these environments are directly connected to the continental shelves, which results in a high concentration of plastic and micro plastic accumulation and therefore the biodegradation by its specific microorganism communities has to be addressed (Harris et al., 2023; Peng et al., 2018).

2.2. Nutrient sources

The vast majority of the aforementioned environments are inhabited by heterotrophic organisms, i.e. organisms that feed on organic matter. A few rare exceptions exist, such as the chemoautotrophic communities initially found near hydrothermal vents and cold seeps (Burd and Thomson, 2022; Danovaro et al., 2014; Jannasch, 1985) but they account for a small fraction of the deep-sea fauna in the majority of the deep-sea environments and are therefore not directly relevant for this study.

In the abyssal zone, organic matter mainly originates from epipelagic zones (upper layers of the oceans) (Ramirez-Llodra et al., 2010). The organic matter from these upper layers is primarily composed of aggregates commonly referred to as particulate organic matter (POM). These particles consist of organic waste, mainly derived from photosynthesis performed by phytoplankton (Iversen, 2023). These aggregates can be transported to the depths through various physical mechanisms, commonly known as marine snow (Sarmiento, 2006a). They are degraded and remobilized progressively in the water column and only a small portion reaches the seafloor (25 %) (Sarmiento, 2006b). Once they reach the seafloor, they are mineralised by deep-sea microorganism communities, which are composed of diverse bacteria, archaea, and eukarya (D'Hondt et al., 2019; LaRowe et al., 2020).

In addition to organic matter from the epipelagic zones, the continental slopes receive a significant amount of nutrients from terrestrial sources (Regnier et al., 2022). These nutrients are transported via the continental shelf by lateral currents (Levin and Sibuet, 2012; Puig et al., 2014). A large proportion of these nutrients is consumed via the aforementioned pathways by organisms that inhabit these environments. However, some of this nutrient matter ultimately reaches the abyssal zones, where it is then transported laterally by various currents present in these deep-sea areas.

The deep-sea fauna thus predominantly feeds on a diffuse supply of particulate organic matter (POM). However, these environments have been observed to occasionally receive large quantities of organic matter (Stockton and DeLaca, 1982) through the fall of pelagic macrofauna (Li et al., 2022) (fish, whales, etc.) or sunken wood (Bienhold et al., 2013). Although rare and negligible in terms of nutrient input compared to marine snow, these events have a significant impact on local biodiversity (Smith, 2006). They are particularly interesting for this review as they illustrate the mechanisms of degradation of macroscopic sources of organic matter that biodegradable materials are likely to encounter during their degradation, which display significant differences with the degradation of POM (see the next section).

3. Biodegradation processes in deep-sea environments

The investigation of biodegradation processes of industrial potentially biodegradable polymers in deep-sea environments is an area of research that is understudied. To the authors' knowledge only two studies have been conducted on this subject (discussed below). However, studies from the biological and archaeological sciences provide valuable insights that are highly relevant for understanding the potential biodegradation processes occurring in deep-sea environments on the biodegradable polymers under consideration. This section presents a review of studies performed on the biodegradation of two types of macroscopic organic matter in deep-sea environments: wood and whale falls. It then discusses studies conducted on the degradation of conventional plastics and the limited number of studies conducted on the biodegradation of alternative biopolymers. Finally factors influencing each biodegradation mechanism are identified and their potential impact is discussed.

3.1. *Organic fall*

Organic falls are important for deep-sea ecosystems as they differ significantly from the typical flux of organic matter from marine snow (cf. Section 2.2 Nutrient sources). These events have been the subject of extensive research since the 1872 Challenger expedition recovered fragments of wood in the Pacific Ocean (Murray, 1895). Similar scientific expeditions were conducted in the second half of the 20th century (Wolff, 1979). The subject was revisited again in the early 21st century with the discovery of a genetic link between the chemosynthetic fauna of hydrothermal vents and cold seeps and the fauna present on these organic falls (wood and whales) (Distel et al., 2000). These studies have provided several key insights. (i) They have led to the discovery of a large number of benthic species and the characterisation and study of their behaviour in the ecosystems generated by these organic falls. (ii) They have brought a deeper understanding of how these communities benefit from the organic matter contained in these falls, and hence of their biodegradation processes. (iii) They showed that these falls play an important role in the connectivity of specialised species across the oceans, and that they are not isolated phenomena specific to geographical zones (e.g. wooded land areas for wood falls).

3.1.1. *Sunken wood*

Wood is of particular interest in this review because it is a structural composite material composed of 90–99 % of natural polymers subjected to enzymatic lysis of their chemical bonds (Pournou, 2020a). Its structure however is much more complex than industrial polymers: wood is hierarchical, porous, and anisotropic comprising a variety of cell types at different length scales, including macro- and microscale cells, cellulose fibrils, and molecular cellulose chains (Fig. 4) (Chen et al., 2020; Ek et al., 2009; Pournou, 2020a). Wood is composed of four layers, which include bark (which provides protection), phloem (which facilitates the transport of nutrients), cambium (which is responsible for cell division), and xylem (which is responsible for the transport of water and dissolved substances) (Fig. 4A). The structure of its tissues varies according to their function, which may be to provide support, facilitate transport, or serve a storage purpose. Its primary components are cellulose (a large linear molecule, highly crystalline, 40–45 % in proportion), hemicelluloses (a smaller molecule, semi-crystalline, 25–50 %), and lignin (large 3D molecules, amorphous, 16–31 %). Large variations in proportion are observed depending on the species, the cell type, and the part of the tree (Dinwoodie, 2000; Schwarze, 2007; Van Dam and Gorshkova, 2003).

The biodegradation of wood in deepsea environments has not been studied within the field of material science, but from a biological and an archaeological perspective. The literature on this subject is extensive and provides highly interesting insights into some of the biodegradation mechanisms involved. Archaeological studies have been conducted with the objective of describing the degradation mechanisms in order to facilitate the preservation of shipwrecks that have retained their structural integrity for several hundred years (Broda and Hill, 2021; Pournou, 2020b; Treu et al., 2019). More recently, biological studies have focused on these falls due to the substantial amount of organic matter present in a sunken trunk, which is likely to create habitats for numerous benthic species (Wolff, 1979).

These studies have reported biodegradation in different locations (e.g. *Fig. 5*) and identified the majority of the mechanisms by which wood is biodegraded. These processes comprise a series of steps, well defined in the work of Pop Ristova et al., 2017 in accordance with the literature on the subject (Bernardino et al., 2010; Bienhold et al., 2013; Fagervold et al., 2014; Kalenitchenko et al., 2018a; Palacios et al., 2009). The initial stage of the process involves the colonisation of the fall by macrofauna that are specialised in wood decomposition, predominantly wood-boring bivalves. These organisms create galleries, fragment the wood and disperse organic matter in the form of wood chips on and around the falls. Subsequently, a diverse range of macroorganisms are attracted to the developing biomass. The fauna present can vary considerably depending on the location of the fall. Studies have documented the presence of annelids, crustaceans (copepods, isopods and galatheids), sea urchins and starfish (Harbour et al., 2021; Judge and

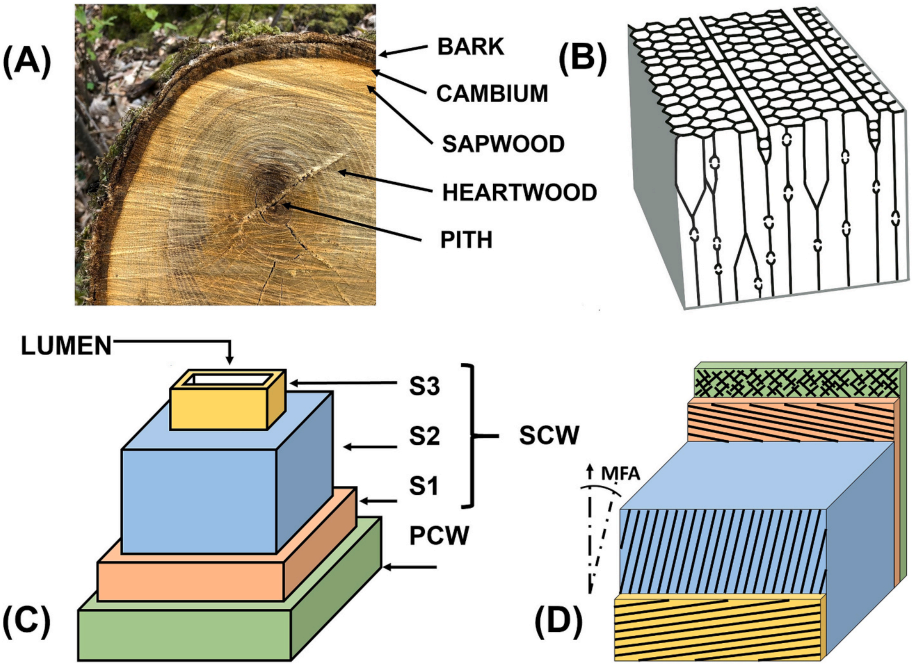

Fig. 4. Schematic representations of A) the different parts of a trunk. Beginning at the outside of the tree is the outer bark). Next is the inner bark and then the vascular cambium, which is too narrow to be seen at this magnification. Inside the vascular cambium is the sapwood, which is easily differentiated from the heartwood that is located at the interior. At the centre of the trunk is the pith, which is barely discernible, at the center of the heartwood. B) the porous structure, C) the multilayer composition of an elementary fibre and D) the orientation of the cellulose fibrils in the different layers (characterised by the microfibrillar angle (MFA), defined as the angle that microfibrils form relative to the fibre axis).

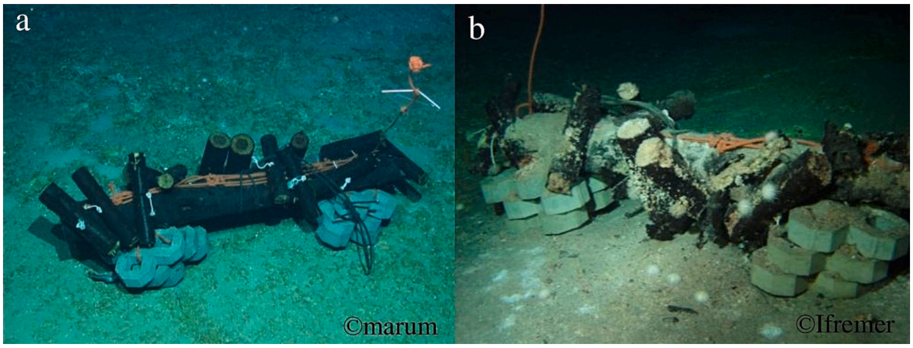

Fig. 5. Douglas logs, (a) just deposed (b) after 1 year of degradation.
Nile Fan, 1700 m, from Pop Ristova et al. (2017).

Barry, 2016; Samadi et al., 2010; Wolff, 1979). The amount of biomass peaks and then gradually declines as the wood decomposes (Pop Ristova et al., 2017). During these steps the wood is also colonised by micro-organisms. A biofilm forms at the wood/water interface and rapidly penetrates the wood, thanks to the specialised macrofauna identified in the first step. These microorganism communities change considerably over time, in a similar way to the macro-organisms. Initially, specialised micro-organisms capable of degrading cellulose are in the majority (Pop Ristova et al., 2017). The dissolved oxygen level drops rapidly at the wood surface and the biofilm is modified: sulphur-based bacteria appear and the bacterial community resembles the chemosynthetic ecosystems around hydrothermal sources (Kalenitchenko et al., 2018a; Pop Ristova et al., 2017). Once the wood is completely decomposed, the bacterial biomass decreases, as does the macroscopic biomass.

The deep ocean environmental conditions do not allow significant abiotic molecular fragmentation of the polymeric constituents of woods: lysis kinetics are extremely slow due to low temperature and low sensitivity to salt, and pressure. Therefore, the primary factor influencing the fragmentation mechanisms, which are essential for the ultimate assimilation, is biotic (Broda and Hill, 2021; Kim and Singh, 2016) and depends on the fauna that colonizes the wood. Several factors affect the colonisation; the location to which the wood sinks has a major influence: first the ocean basin (Kalenitchenko et al., 2015; Pop Ristova et al., 2017; Romano et al., 2020), then the depth (Young et al., 2022) and the type of deep-sea environments: abyssal plain, submarine canyon, near a hydrothermal source or a cold seep, … (Fagervold et al., 2014; Pereira et al., 2022). Second, the type of wood has a strong influence on the microfauna (Kalenitchenko et al., 2015; Palacios et al., 2009) and the macrofauna (Judge and Barry, 2016) that colonize it. To the authors' knowledge no firm conclusions have been drawn on this last point: Eriksen et al., 2017 (Eriksen et al., 2017) suggest that this could be due to the amount of cellulose and the density but the amount of lignin could also play a role.

A key factor is the specialised species that initiate the decomposition process (Kalenitchenko et al., 2018a). These species are mainly wood-boring bivalves of the Xylophagaidae family. They feed on wood by digging tunnels. This releases organic matter around the wood and enriches sediments in a radius of tens of centimetres (Bernardino et al., 2010). The released organic matter, in the form of faecal pellets, contains specific microorganisms that differ from those on the wood surface (Fagervold et al., 2014). In addition, the galleries attract opportunist macrofauna (Young et al., 2022) and accelerate the installation of chemosynthetic microorganisms inside the wood (Kalenitchenko et al., 2018b). Bivalves increase the biodiversity on the wood and degrade its structure significantly. Pop Ristova et al. (2017) and Kalenitchenko et al. (2018a) observed that in the absence of these specialist species, some degradation still occurs, but the kinetics are much slower and biodiversity is reduced.

Several studies have shown that colonisation by specialist species occurs even in sites far from the coast (Amon et al., 2017; Romano et al., 2020). It appears that, in the vast majority of cases, land-based organic wastes can be degraded in deep benthic ecosystems. However there are some exceptions: a number of sunken ships have preserved their structure after several hundred years in the ocean (Jurgens and Blanchette, 2003; Sandström et al., 2002). These shipwrecks have been extensively studied by archaeologists, as part of the preservation of cultural heritage. They have been found in areas with very low levels of oxygen, buried in the sediment (Björdal and Nilsson, 2008) mainly on continental shelves. These conditions do not allow colonisation by specialised macrofauna. Despite these conditions hardly conducive to life, the wood was never completely intact: the cellulose present in the wood cells was largely consumed, leaving only a skeleton composed of lamellae and external cell walls (mainly lignin). This explains why the structures retained their shape. Moreover, these studies have precisely characterised how microorganisms degrade the complex structure of wood: there are several modes of degradation, summarized in Jurgens and Blanchette (2003) and Pournou (2020b). To our knowledge, these degradation processes have never been successfully reproduced in the laboratory, and the organisms responsible for them have not been precisely identified.

The degradation of sunken wood has been the subject of research and analysis for several decades, and while the processes involved are now partially understood, there are still some areas of uncertainty. For instance, while the main actors of degradation have been identified in the deep sea, there is a lack of clarity regarding the microorganisms involved, their interactions within biofilms, and the environmental conditions that facilitate this degradation. Furthermore, the mechanisms underlying the degradation of lignin in deep-sea environments remain poorly understood. In coastal and terrestrial environments fungi communities have been identified as the primary agent although some uncertainty remains (Pournou, 2020b). In deep-sea environments, fungi have also been observed on sunken wood, yet their role in the degradation of lignin remains unknown (Samadi et al., 2010; Wolff, 1979). Reviews detailing the degradation of wood at archaeological sites do not provide insights into what happens to the wood particles rejected by the specialist macrofauna on the sediments and the surface of the wood. These wood particles may be mineralised by a consortium of microorganisms or subsequently stored in the sediments. Therefore, it is impossible to conclude regarding the total assimilation of the organic matter initially contained in the degraded wood. Only the deterioration of wood has been demonstrated to date, with kinetics highly dependent on the fauna colonising the sunken wood and therefore the environmental properties of the location of the fall (biological, physical, and chemical).

3.1.2. *Whale falls*

Whale falls represent another organic fall that has been extensively studied by the scientific community. They primarily consist of fresh flesh

(87–92 % by mass) and bones (3.5–5 % by mass) (Robineau and Buffrénil, 1993). These two components contain few polymers (only proteins) but are predominantly organic matter, hence carbon chains. Fresh flesh is primarily composed of lipids and proteins (Smith, 2006) while bones are composite materials containing collagen (a protein) and lipids (at variable, sometimes significant, amounts ranging from 5 to 50 %) in an inorganic apatite matrix (Wysokowski et al., 2020). The estimated amount of carbon introduced into the deep sea by these falls is 1.6×10^6 g for a 40-ton carcass (Smith, 2006). This is a considerable contribution, equivalent to the carbon input from 100 to 200 years of the flux from epipelagic zones over 1 ha (Smith and Baco, 2003). Analysing the degradation of these falls offers insights into the processes of carbon remobilisation, which is pertinent to our study.

In a similar approach to wood falls, scientists initially focused on the fauna that colonizes these falls, leading to the discovery of previously unknown species (Smith and Baco, 2003). Knowledge then significantly expanded in the late 20th century with the discovery of chemosynthetic-based faunal communities on a carcass found in the NE Pacific; this isolated local ecosystem exhibited strong similarities to communities observed near hydrothermal vents (Smith et al., 1989). A number of subsequent studies on other whale falls have corroborated this discovery (Dewing et al., 1997; McLean, 1992; Naganuma et al., 1996). This has generated considerable interest from the marine biology scientific community: whale falls are believed to play a crucial role in benthic biodiversity and the dispersal of bacterial and chemosynthetic species across the oceans. Since then, further carcasses have been found and studied, and artificial in-situ immersions with ongoing monitoring have been conducted, as illustrated in *Fig. 6*. Smith et al., 2015 (Smith et al., 2015) provide a comprehensive review of the current state of knowledge on the subject. The main points are presented below.

Whale falls serve as habitats for an exceptional amount of biomass in the deep sea. Each stage of the decomposition process harbours a multitude of distinct species. Initially, mobile scavengers, including hagfish, sharks, and crustaceans, feed on the flesh, dispersing organic matter throughout the carcass, enriching the surrounding sediments (Goffredi and Orphan, 2010; Naganuma et al., 1996; Treude et al., 2009). Subsequently, opportunistic macrofaunal species, including polychaetes, crustaceans, bivalves, ophiuroids, and echinoids, as well as mainly heterotrophic microorganisms, colonize the skeleton and enriched sediments. This results in a significant increase in biomass around the carcass, which is referred to as the enrichment-opportunist stage. In a similar way to wood falls, the degradation of the skeleton and organic matter in the sediments by heterotrophic microorganisms induces anaerobic conditions locally and the production of sulphide and methane. This supports the colonisation by chemosynthetic microorganisms, which gradually become a more significant proportion of the biofilm community (sulfophilic stage) (Goffredi and Orphan, 2010; Treude et al., 2009). Smith et al. (Smith et al., 2015) also describe a fourth phase, named the reef stage, when the activity of microbial communities and macrofauna in the sediments ceases, leaving only the biological activity of bone degradation by sulfophilic communities and the presence of suspension-feeding fauna using bones as a substrate. To the best of our knowledge, this stage has not been fully characterised.

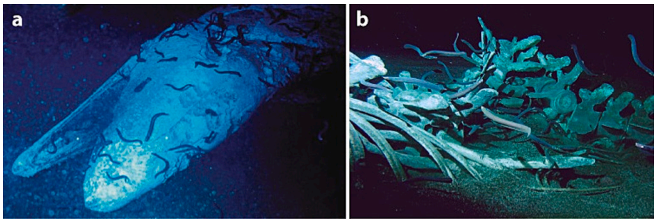

Fig. 6. Whale falls, (a) just deposed (b) after 1.5 years of degradation. Santa Cruz Basin, 1675 m, from Smith et al. (2015). ©2015 by Annual Reviews. Reprinted with permission.

The kinetics of these degradation stages depend on multiple environmental variables including the macro and micro fauna that colonised the fall, the size of the carcass, depth, currents, or turbidity. Higgs et al. (Higgs et al., 2011a) demonstrate that the presence of Osedax worms from the family of siboglinidae can significantly accelerate bone degradation thereby advancing the sulfophilic stage. Higgs et al. (b) (Higgs et al., 2011b) and Amon et al. (Amon et al., 2013) showed that the structure of bones influences the fauna present and, consequently, the degradation kinetics. The complete degradation of the carcass can therefore take anywhere from a few years to several hundred years, depending on all these factors.

3.1.3. Key points

These two examples of biodegradation processes in deep sea environments provide three key points. (i) Regardless of the specific environments under study (abyssal zone, continental slopes, colds seeps, hydrothermal vent), wood and whale falls are being degraded. This indicates that, despite these falls being rare events, microorganisms capable of degrading lignocellulosic materials and bones or flesh are present in most deep-sea environments. This raises significant questions regarding their ability to survive until such events occur and their capacity to colonize these falls when they do. These properties of deep-sea microorganisms could be of significant importance for industrial polymer degraders, yet they remain a crucial knowledge gap in the field of deep-sea ecology (Gary et al., 2020; Hilário et al., 2015). (ii) During the biodegradation of these falls the consumption of oxygen exceeds the quantity provided via the bottom currents inducing anoxic conditions and an important shift in bacterial communities. It seems probable that a similar phenomenon will occur in the case of the biodegradation of a deep-sea biodegradable polymer, potentially excluding aerobic communities from the environment of degradation. (iii) A key factor influencing the degradation rate appears to be the presence of specialised macro fauna, which significantly accelerates the breakdown of the falls. In the case of whale bones, the degradation may not occur without the presence of this specialised fauna to enhance the deterioration of the material.

3.2. Deep-sea degradation of structural polymer materials

3.2.1. Conventional plastics

To the authors' knowledge, the first study on the degradation of conventional plastics in deep-sea environments was conducted in 1965. Muraoka et al. (Muraoka, 1965) immersed a range of materials, including various types of wood, plastic (PS, PP, PC, PE, PA6), and metal for a period exceeding one year at a depth of 840 m on the continental slope off the coast of California. Plastics, in the form of injection-moulded samples, ropes and electrical wire sheaths, demonstrated the capacity to retain their mechanical properties, with no visible signs of degradation. Since then two studies on plastic waste recovered after several decades in the deep sea are worthy of mention. Zhang and Peng recovered a variety of plastic macro-litter items from 22 distinct locations in the South China Sea, predominantly from continental slopes and trough environments (Zhang and Peng, 2022). Their findings indicated the presence of minimal signs of degradation on PE samples, and the absence of any degradation on the other conventional polymers tested (PP, PET, PVC, and PS). Observations were made on more than 100 pieces of plastic recovered, after an estimated period of ageing spanning several decades. In a similar study, Krause et al. observed no evidence of surface degradation on all recovered plastics at a depth of 4100 m in the abyssal zones of the Peru Basin, located in the South-east Equatorial Pacific, after more than two decades in the marine environment.(Krause et al., 2020).

This brief paragraph illustrates the limited knowledge regarding the degradation and biodegradation of conventional plastics in deep-sea environments. The three studies presented above indicate that abyssal plains do not provide the conditions conducive to degradation of conventional plastics. Studies on fouling (e.g. (Agostini et al., 2021; Kelly et al., 2022; Woodall et al., 2018)) and monitoring of plastic litter (e.g. (Amon et al., 2020; Angiolillo et al., 2021; Nakajima et al., 2021)) in different deep-sea environments did not indicate any signs of degradation in the samples observed or recovered. Furthermore, monitoring studies demonstrate a significant increase in the pollution of the deep sea, including both macro-plastics and micro-plastics. Consequently, the initial studies on conventional polymers in the deep sea indicate that these materials are persistent in deep-sea environments, with slow rates of molecular fragmentation and no proof of mineralisation, resulting in an accumulation in deep-sea sediments.

3.2.2. *Biodegradable polymer*

To date only four studies have been conducted on the biodegradation in deep-sea environments of biopolymers, candidates to substitute conventional plastics. Omura et al. immersed a wide variety of biopolyesters (including several types of PHAs, PBS, PBAT, PBSA, PLA, and PCL), conventional plastics (PP, PS, PE, PET) and cellulose derivatives (Omura et al., 2024) in different deep-sea environments for periods of ageing from 3 to 14 months. The study was conducted at five sites in three different deep-sea environments, including two sites in the abyssal plain (5500 and 5550 m depths), two sites on the continental slope (750 m deep), and one site near a hydrothermal vent (1300 m depth). It provides evidence of PHA biodegradation with significant mass losses and surface alteration, while other biopolyesters displayed minimal or no signs of degradation during the same ageing period. Conventional plastics and PLA were intact after the experiments. Hyodo et al. demonstrate similar results after the immersion of PHA microbeads for 5 months in one of those previous continental slope sites (Hyodo et al., 2024). Two other studies under semi-realistic immersion conditions show similar results: Sekiguchi et al. (Sekiguchi et al., 2011a) and Hachisuka et al. (Hachisuka et al., 2023). In the first study the same types of biopolyesters were immersed for a period of ageing of one year in laboratory conditions using deep-sea water pumped from a depth of 300 m and continuously replenished, at atmospheric pressure, and at room temperature. The second study focused on various types of PHAs and PLA, under similar immersion conditions (seawater from two sites: 24 m and 397 m deep, mean temperature 10 °C, at atmospheric pressure) for a period of ageing of 7 months. Although there are significant limitations due to temperature and pressure variations, the polyesters studied in these two latter studies were exposed to deep-sea microorganisms, with nutrient conditions relatively representative of their natural habitat. In the first study, PHAs and PCL exhibited pronounced signs of degradation after a six-week immersion period, whereas PBS samples displayed no evidence of degradation. The second study yielded similar findings, with degradation observed in PHAs samples but not in PLA samples.

The results of the four studies do not allow the formulation of definitive conclusions. Further studies are required to confirm the biodegradability of the materials under consideration, specifically PHAs and other biopolyesters. However, PLA did not show any signs of degradation in six distinct deep-sea environments, thereby indicating that it is not a suitable candidate for marine biodegradation. The other polyesters, namely PBS, PBAT, PBSA and PCL, should also be viewed with caution, given that they exhibit very limited degradation rates in these same environments. In certain cases, such as in the case of both PBS and PBSA in abyssal sites, there was no observable degradation. These results support previous concerns raised in coastal environments (Harrison et al., 2018) and call for more investigations.

3.3. *Factors influencing deep-sea degradation*

Although research into the biodegradation of polymers in deep-sea environments is scarce, existing literature offers sufficient insights to facilitate an investigation into the factors influencing these processes. The following section outlines these factors for each of the three mechanisms involved in the biodegradation process, namely deterioration, molecular fragmentation and assimilation.

3.3.1. *Deterioration*

The deterioration process is characterised by the breakdown of the studied material, driven by various factors that can be abiotic or biotic (i.e. driven by the action of living organisms or not) (Lucas et al., 2008) (Fig. 2). In coastal marine environments, this process is primarily accelerated by mechanical stresses such as wave action and tidal forces. However, these phenomena are absent in deep-sea environments. Nevertheless, a number of additional factors may also be involved in the deterioration of the materials under consideration.

First, the role of hydrostatic pressure must be considered. Although the impact of hydrostatic pressure on polymers remains a relatively under-researched topic, a number of studies have been conducted in this area (Hoppel et al., 1995). A first consideration is the influence of pressure on the diffusion of moisture into the polymer. Published results suggest that in a well-consolidated polymer or composite the influence of pressures up to 500 bars has low/no impact (Humeau et al., 2016; Whitaker et al., 1991). However, if voids are present after manufacture then adding pressure will fill them and increase overall water content (Humeau et al., 2016). A second concern is material embrittlement, which can reduce resistance to other mechanical stresses. Choqueuse and Davies observed little effect up to 1000 bars (Choqueuse and Davies, 2014; Davies et al., 2004), though published work has indicated embrittlement effects at higher pressures (Aulova et al., 2019; Mears et al., 1969).

Another factor that could influence the biodeterioration of plastic litter in the deep-sea is the presence of high-intensity disturbance events. The best-characterised events are benthic storms, which regularly affect abyssal zones, and slope failures, which impact continental slopes and continental rises (Harris, 2014). These events are thought to play a key role in deep-sea ecological dynamics (Harris, 2014). Benthic storms are more frequent in regions with strong surface currents, such as the Gulf Stream and the Agulhas Current. However, they are postulated to be ubiquitous across all ocean basins. These storms are characterised by significant increases in bottom current speeds, which can reach up to 0.7 m/s (equivalent to a 9 $m.s^{-1}$ windstorm), and can disturb benthic ecosystems by resuspending sediments, larvae, and juveniles (Cronin et al., 2013; Harris, 2014). Another disturbance event is slope failure. These occur on continental slope and rise environments and are caused by the accumulation of sediments originating from the continental shelf. The frequency of occurrence decreases with depth, from approximately once per decade at the top of the slope to once every thousand years for the continental rise. The intensity of these events also increases with depth.

The limited number of studies that have been conducted on the ageing of conventional plastics submerged or recovered during observational operations, as previously mentioned, tend to minimise the potential impact of abiotic factors. These materials exhibited no discernible degradation after one year of ageing, as observed by Muraoka et al. (Muraoka, 1965) Similarly, over several decades, Zhang and Peng and Krause et al. noted no significant degradation of the materials under study (Krause et al., 2020; Zhang and Peng, 2022). This evidence suggests that abiotic factors are negligible; however, further investigation is needed to confirm this hypothesis.

An additional factor with the potential to impact biodeterioration processes is meiofauna and macrofauna activity. In studies focused on organic falls degradation, this factor plays a significant role in the biodegradation process. These phenomena have not been observed during the biodegradation of synthetic/industrial polymers or biopolymers in coastal marine environments, nor in the four studies on deep-sea biodegradation previously cited. However, Muraoka et al. observed the degradation of some samples by woodborer bivalves, with even conventional plastics affected (PC, PS, PE, cellulose acetate) (Muraoka, 1965). It was observed that only the samples in direct contact with the wood samples were affected, and it appeared that the bivalves initially colonised the wood. The presence of lignocellulosic materials, such as the addition of natural fibre fillers, could potentially allow colonisation by these organisms and significantly enhance both the deterioration and biodegradation processes.

3.3.2. *Molecular fragmentation*

The breaking of polymer carbon chains is a highly energy-intensive reaction, which is why conventional plastics persist in most natural environments. The durability of the most common conventional plastics has been extensively documented in their terrestrial and coastal service environments. In these environments, the most common degradations pathways are molecular fragmentation via hydrolysis and/or oxidation and key degradation factors are temperature and UV exposure (Allara, 1975; Scott, 1995; Verdu, 2012). In the deep sea, the temperature is low and there is no exposure to UV radiation (cf Section 2.1 Deep-sea environments), therefore the abiotic molecular fragmentation is extremely slow, resulting in very slow degradation kinetics (Choqueuse and Davies, 2014; Oluwoye et al., 2023).

Biodegradable materials are sensitive to these chain-cleavage reactions in the presence of extracellular enzymes (biofragmentation). These enzymes are secreted by microorganisms within the biofilm, leading to a notable acceleration of the molecular fragmentation kinetics. (Laycock et al., 2017). For most promising biodegradable materials, chain breakage occurs at ester groups (polyesters) or glycosidic linkages (for polysaccharides and lignocellulosic materials) (Laycock et al., 2017; Pournou, 2020a). Therefore, the presence of organisms capable of secreting these enzymes in deep-sea environments is the predominant factor influencing this mechanism. However, this remains poorly understood due to the limited knowledge about the microbial communities in these environments.

Studies on wood biodegradation have demonstrated that microorganisms capable of fragmenting lignocellulosic materials are present in most deep-sea environments (cf. Section 3.1.1 Sunken wood). With regard to biopolyesters, the four existing studies encompass only eight locations, all situated in the western Pacific Ocean, in proximity to Japan (Hachisuka et al., 2023; Hyodo et al., 2024; Omura et al., 2024; Sekiguchi et al., 2011b). Nevertheless, these studies have observed the occurrence of biofragmentation mechanisms in PHAs and, to a lesser extent, in other polyesters, including PBAT, PBS, PBSAT, and PCL. These mechanisms are associated with surface degradation, which is characterised by the formation of holes (Fig. 7) (Deroiné et al., 2015; Laycock et al., 2017; Omura et al., 2024). In their study, Omura et al. conducted a comparative analysis between the biofilm communities present on degraded materials, which have in their genome the genes enabling the secretion of enzymes to degrade these materials, and the available data on sediment communities. The authors conclude that these microorganisms are present in many ocean basins and that there is a high probability that the results obtained in their study can be generalised. However, many questions remain regarding the conditions required for their establishment in biofilms and the activation of these functions (extracellular enzyme secretion and utilisation of oligomers through intracellular enzymes). These questions parallel the challenges faced in studying biodegradation in coastal marine environments for any generalisation and transferability (Albright and Chai, 2021; Haider et al., 2019; Harrison et al., 2018).

3.3.3. *Assimilation*

The factors influencing assimilation are similar to those affecting biofragmentation. This phase is dependent on the presence of microorganisms with the capacity to mineralise or assimilate the oligomers that result from the degradation of the material in question. It is therefore imperative that these microorganisms are present within the biofilm, and that the molecular fragmentation process has yielded degradation products of a sufficiently small size to penetrate the cell membranes of these organisms (Wang et al., 2021). To date, no study has demonstrated the assimilation of degraded materials in deep-sea environments, whether from organic falls or biopolyesters, notably because of an important gap in technical means and methodologies (discussed in the next section).

3.3.4. *Colonisation*

Biofragmentation and bioassimilation are directly dependent on the communities available in the surrounding environments and more specifically in the biofilm that forms on the sample. The formation and growth of the biofilm is a highly complex process, influenced by many factors. The most recent advances in this field were summarized by Dang and Lovell, 2016 and by Qian et al., 2022. Similarly to biodegradation studies, the literature on biofilm in deep-sea environments is sparse. Several biological studies have investigated the phenomenon, but at very specific sites that are not representative of the deep-ocean (cold seep, hydrothermal vent, cf. Section 2.1 Deep-sea environments), with the aim of discovering specific bacteria (Guezennec et al., 1998; Lee et al., 2015; Zhang et al., 2015). Few studies have been conducted in abyssal regions or in the continental slopes (Agostini et al., 2021; Bellou et al., 2020, 2012; Kelly et al., 2022; Meier et al., 2013). A number of

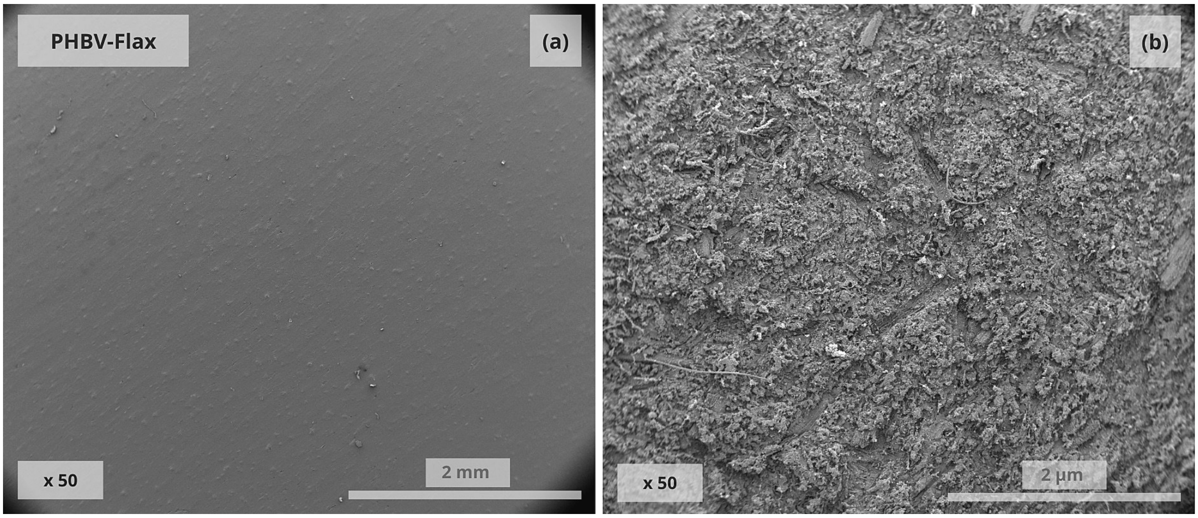

Fig. 7. SEM images, PHBV flax composite surface, (a) before degradation (b) after 1 year of immersion at the Lampaul submarine canyon, Atlantic West, 850 m, authors' observations.

factors have been identified as being of particular significance when assessing microbial communities in these environments:

- The nature of the substrate. Inorganic mineral and petroleum-based plastics biofilms show different communities (Agostini et al., 2021; Meier et al., 2013; Woodall et al., 2018). However, within these two categories of materials, the communities are similar (Agostini et al., 2021; Krause et al., 2020). Significant differences have been observed between biodegradable and inert substrates (Omura et al., 2024), with similar observations made in coastal environments (Cheng et al., 2022; Qian et al., 2022). These differences could be attributed to the presence of specialist microorganisms capable of deteriorating and mineralising the substrate, which in turn influences the entire community.
- The timescale. As previously found in epipelagic zones, the biofilm development is fast and significant microbial community differences have been observed in the initial stage of the colonisation (first days) (Guezennec et al., 1998; Zhang et al., 2015). The stabilisation of the biofilm microorganism's communities is thought to take a few days (Qian et al., 2022) but this has never been confirmed in deep-sea environments. Over longer periods the seasonality plays a role (Bellou et al., 2020).
- Oxygen availability. The absence of oxygen is an excluding factor for many microorganisms. In the majority of cases observed in deep-sea environments, oxygen is present and aerobic microorganisms are present within the biofilm (Krause et al., 2020; Omura et al., 2024). Nevertheless, when the substrate is biodegradable, several studies have demonstrated that oxygen consumption by the microorganisms responsible for the degradation of the material can induce anaerobic conditions locally. This phenomenon has been well characterised in studies of organic falls (Sections 3.1.1 and 3.1.2) and the shift to anaerobic communities observed by Omura et al. suggest similar phenomena for biopolyester biodegradation (Omura et al., 2024).
- The location. Strong differences in biofilm communities have been observed in the different types of deep-sea environments, especially between chemosynthetic environments (hydrothermal sources, cold seeps or brine pools) and abyssal plain and continental slopes. (Lee et al., 2015; Zhang et al., 2015). The pressure and the temperature can exclude some microorganisms and therefore differences are observed between the upper region of the continental slope and the abyssal zones (Levin and Sibuet, 2012). And within the same type of environment, differences are also observed between ocean basins.

There are numerous unanswered questions regarding biofouling phenomena in marine environments: (i) The mechanisms by which species move in the oceans and their distribution in the different environments (Hilário et al., 2015) (ii) The processes by which species are selected within the biofilm (Qian et al., 2022) (iii) The nature of the interactions within the biofilm. An improved understanding of these phenomena is needed as it could lead to more accurate predictions of the presence of degraders of a material in a given environment (coastal or deep-sea) (Qian et al., 2022).

3.4. Limits

Despite the limited number of studies, key aspects of biodegradation mechanisms in deep-sea environments are partially understood and/or hypothesised thanks to transferability from other degradation environments and studies in other scientific fields such as biology or archaeology. However, there are still important gaps in our knowledge that prevent us from drawing general conclusions: the mineralisation of the most promising materials has never been studied in deep-sea environments, and the colonisation by microbial degraders in each deep-sea environment cannot be stated with certainty, given that biological processes in these environments are not yet fully understood. It is imperative that both of these points be addressed before any material is claimed to be biodegradable in a marine environment. The following section will describe the available methods for studying these topics and suggest methodologies that may be of interest, along with precautions that should be taken.

4. Experimental approach

Scientific investigations of the biodegradation of a material in a specific environment employ two principal methodologies. The first involves in-situ ageing, whereby materials are immersed at sea and periodically sampled, followed by laboratory characterisation of the changes in the properties of the materials and identification of the organisms present in the biofilm. The second involves conducting laboratory tests with the objective of accelerating the degradation mechanisms and observing specifically the impact of certain factors of interest.

4.1. In situ ageing

The development of technologies and experimental approaches to explore the deep sea has been significantly enhanced since the 1960s with the introduction of scientific submersibles. These vehicles facilitate the observation, deployment, and retrieval of materials on the ocean floor, with depths currently reaching down to the deepest areas of the ocean (Chiba et al., 2018). These operations have been further facilitated by the establishment of underwater observatories in the 2010s (e.g. European Multidisciplinary Seafloor and water column Observatory (EMSO) in Europe (Favali and Beranzoli, 2009), Ocean Networks Canada in Canada and Ocean Observatory Initiative in the United-States (Best et al., 2007)).

Initial studies of deep-sea degradation have been conducted on samples recovered from the deep-sea floor during observation campaigns (Wolff, 1979). These studies allow the characterisation of degradation of samples aged for long periods, with slow kinetics of degradation (Amon et al., 2020; Krause et al., 2020; Zhang and Peng, 2022). However they are limited, they depend on the available plastic litter in the environments investigated and ageing histories can be difficult to quantify (Zhang and Peng, 2022). The immersion of materials in situ allows a wide variety of more targeted studies. These include the investigation of the impact of specific factors; substrate nature (Bellou et al., 2012; Higgs et al., 2011a; Judge and Barry, 2016; Omura et al., 2024), ageing time (Bellou et al., 2020; Kalenitchenko et al., 2015; Pop Ristova et al., 2017), degradation environment (Kalenitchenko et al., 2015; Omura et al., 2024; Pop Ristova et al., 2017), substrate orientation (Bellou et al., 2020, 2012). Environmental parameters such as temperature, oxygen levels, pressure, or salinity can be measured (Bienhold et al., 2013; Kalenitchenko et al., 2018b). These studies require highly developed testing instruments and have significant operational costs (e.g. ROV, research vessel, human resources, sensors adapted to deep-sea environments). Several laboratories have specialised in studying these ecosystems and leading sea-going expeditions. However, to our knowledge, few are working on the mechanisms of degradation/biodegradation of plastics materials and/or their biodegradable substitutes.

Two methods are available for the immersion and recovery of samples. (i) A deep sea submersible (manned, ROV or AUV) manually places and recovers the samples on the seafloor (Omura et al., 2024; Pop Ristova et al., 2017), or (ii) Samples are placed on a structure that is then deployed from a ship (Muraoka, 1965). The latter is more restrictive as samples are positioned on the structure and will be recovered on board during maintenance operations. Subsequently, immersed samples must be either recovered simultaneously or undergo multiple cycles of pressurisation and depressurisation, which is likely to result in significant damage to the micro-organism communities (Cario et al., 2019; Tamburini, 2006). The use of submersibles allows for greater operational flexibility with regard to the duration of deployment, the location of the deployment, and the performance of experimental tests, thanks to the greater number of devices that have been developed for these vessels (Cario et al., 2019; Jamieson et al., 2013). The deployment and recovery protocols must be adapted in accordance with the specific requirements for each experiment and the resources that are available (including the type and size of the submersible, the number of personnel available, and the availability of a suitable vessel). A comprehensive understanding of the processes of biodegradation requires a transdisciplinary approach, which entails biological and physico-chemical characterisations of the biofilm and the material being investigated. The constraints induced by these characterisations on these protocols are outlined in the next paragraph.

4.1.1. *Biological experimentation*

Biological studies in the deep sea present a significant technical challenge. These studies require careful sample preservation and the avoidance of contamination throughout the entire sampling and storage procedure until laboratory analysis. The crucial stage in the process is the retrieval of samples from the ocean depths to the boat. In initial studies samples were recovered without the use of isolation devices and then rinsed with filtered seawater in order to minimise the contamination by microorganisms of the upper pelagic layers (Bellou et al., 2020; Kalenitchenko et al., 2018b; Muraoka, 1965). Other studies have used isolation containers, which preserve samples from washing and contamination during the ascent (Bienhold et al., 2013; Cuvelier et al., 2014; Dewing et al., 1997; Omura et al., 2024; Pop Ristova et al., 2017). The majority of biological studies mentioned in this review were conducted via one of these two methods. Nevertheless, some recent studies have demonstrated that the depressurisation that occurs during the sampling process can induce significant bias in the biological characterisations obtained (Edgcomb et al., 2016; Feike et al., 2012; Garel et al., 2019; Wei et al., 2020). Consequently, the most recent reviews on the subject strongly recommend the use of devices that preserve the in situ pressure during the ascent (Cario et al., 2019; Huang et al., 2023). These devices were first developed and utilised in 1976 by Jannasch et al. (1976) and are now reliable and used in numerous deep sea biological studies (Cario et al., 2019; Garel et al., 2019; Shillito et al., 2023). Once on board, samples must be flash frozen and stored at cold temperatures (−20 °C or − 80 °C, depending on the analyses to be performed). All manipulation must be conducted in a sterile environment to prevent contamination. The work environment should be sterilised, and manipulations should be conducted under a laminar flow hood with sterile gloves and tools.

As mentioned above, several reviews advocate more biological considerations in biodegradation studies, and in particular omics characterisations (Shah et al., 2008; Viljakainen and Hug, 2021); these techniques allow the identification of the microbial communities in the biofilm and a better understanding of the mechanisms involved in the degradation processes (Hassan et al., 2022; Kowalczyk et al., 2015; Tiwari et al., 2022). Omics tests include five different methods: metabarcoding and metagenomics, metatranscriptomics, metaproteomics and metabolomics (well described in Lobanov et al. (2022)). The first, metabarcoding and metagenomics, requires DNA sampling of the biofilm. Metabarcoding is a common method, widely developed and used in microbiological studies. Several examples of its application to deep-sea biofilms can be found in the literature (e.g. (Agostini et al., 2021; Bellou et al., 2020; Omura et al., 2024)). Metatranscriptomics is a more recent method that characterises the mRNA present in the biofilm. The post-treatment allows the characterisation of the expressed genes within the biofilm and therefore the synthesised enzyme and the functions available within the biofilm (Huang et al., 2023). This method is more difficult to perform under deep-sea conditions because mRNA is a much less stable molecule than DNA. Metaproteomics (the analysis of protein content) and metabolomics (the study of the metabolome) are methods that are even rarer, they have been used to characterise specific biodegradation processes in the laboratory (Meyer-Cifuentes et al., 2020) but, to our knowledge, they have not yet been used to characterise biological deep-sea communities. These three experiments require a high level of precaution in sampling and storage until laboratory analysis and subsequent sequencing. But the sampling equipment is available (Huang et al., 2023); Mat et al. (2020) successfully sampled mussels directly in RNA, near hydrothermal vents, and sequenced their transcriptomes.

4.1.2. *Physico-chemical and mechanical characterisation*

The constraints for physico-chemical and mechanical experiments in the deep sea are less critical; they are essentially the same as for ageing in other types of environment. Lucas et al. (2008) and Harrison et al. (2018) provide recommendations on marine degradation. (i) Prior to the ageing process, it is essential to validate the manufacturing process to ensure the homogeneity of the samples under study. Furthermore, initial characterisation is required, and the identification of the specimens is recommended. The number of specimens can be significant, and their geometry may be dictated by the test (e.g. tensile test (ISO, 2012)). (ii) The depressurisation occurring during the recovery of the samples may affect the macrostructure of the aged samples, which could induce a bias in the subsequent characterisations. The literature on this subject is limited for injected polymers, but studies conducted on elastomers have demonstrated that there are significant risks of cavitation and cracking during decompression (Jaravel et al., 2011; Schrittesser et al., 2016). (iii) After the recovery of the samples, it is essential to prevent their degradation before characterisation. It is necessary to neutralise biotic agents and to store the samples until characterisation in a protective environment. For biotic agents, samples can be sonicated in distilled water and dried (Omura et al., 2024) or simply rinsed and stored at low temperature (Krause et al., 2020). Freezing is an effective method of stopping microbial activity, although it may also induce modifications to the macrostructure of specimens. The optimal storage conditions will depend on the materials under consideration, and should be determined based on an abiotic degradation study.

4.2. *In vitro ageing*

In the field of experimental ageing, ex-situ experiments have been developed to overcome the higher costs, risks, and variability associated with in situ experiments. This approach allows for the control of environmental variables, thereby enabling the investigation of specific mechanisms of degradation, the impact of specific factors on these mechanisms, and the acceleration of the degradation process. For conventional polymer materials, the most frequently studied factors for deep sea degradation are temperature and pressure (Le Gac et al., 2015; Oluwoye et al., 2023). For example, an increase in the ageing temperature accelerates the kinetics of abiotic hydrolysis, often modelled by an Arrhenius function (Deroiné et al., 2014b). Biodegradation pathways encompass both biotic and abiotic factors, consequently both need to be investigated to conclude on biotic contribution to deterioration and molecular fragmentation. This paragraph reviews the methods available in the literature for studying the impact of these factors on the three mechanisms of the biodegradation process.

4.2.1. *Abiotic factors*

The literature on deep-sea degradation of conventional polymers shows extremely slow degradation kinetics and therefore abiotic factors are expected to have very limited impact on the overall degradation of potential deep-sea biodegradable polymer (sea Section 3.3). However the available literature on the “biopolymers” abiotic degradation is scarce. Some studies in distilled water have investigated the specific impact of temperature at atmospheric pressure and highlighted the importance of this factor for the materials studied (Lucas et al., 2008). See Deroiné et al. (2014b) on PHBV or Le Gué et al. (2024) on a PBSA monofilament. It must be remembered that the response to these parameters strongly depends on the nature of the polymer and its structure

(Lucas et al., 2008).

The effect of hydrostatic pressure should also be considered for these new materials. Equipment is available to perform hydrostatic ageing and mechanical testing at pressures up to 1000 bar (Choqueuse and Davies, 2014; Davies et al., 2004) (example Fig. 8). Low/no effects on embrittlement and water diffusion have been characterised for conventional plastics (Aulova et al., 2019; Choqueuse and Davies, 2014; Humeau et al., 2016; Whitaker et al., 1991) but no investigations have been conducted on biopolymers.

4.2.2. Biotic factors

The laboratory investigation of the biotic factors of marine biodegradation shows a significant knowledge gap. Ex-situ experimentation on biotic factors is the most common approach for characterising the assimilation/mineralisation stage of the biodegradation process in marine environments, (Harrison et al., 2018; Wang et al., 2021). However, as previously stated in Section 1.2 Marine biodegradation, the methods recommended by international standards for biodegradation in marine environment including benthic environments are severely limited (Harrison et al., 2018; Wang et al., 2021). Various reviews have proposed alternative methods that are more representative of the actual degradation environment, calling for more transdisciplinary approaches (Kowalczyk et al., 2015; Shah et al., 2008; Van Rossum, 2021). Other methods from biology and microbiology should be cited. Tests based on 3H-leucine incorporation have been demonstrated to be a good proxy of biodegradation activity by Jacquin et al. (Jacquin et al., 2021) and this is apparently easier to implement than respirometry, used also in (Dussud et al., 2018). And the omics methods, cited above (Section 4.1.1 In situ) are also available.

The difficulties encountered in studying the biotic processes in deep-sea environments are further compounded by (i) the lack of knowledge regarding endemic bacterial communities and (ii) the technical challenges involved in sampling and culturing microorganisms to replicate real degradation conditions. To the authors' knowledge, respirometric ex-situ tests with a representative community of deep-sea organisms has never been performed. However, some promising preliminary work should be cited. Sekiguchi et al. (2011a) and Hachisuka et al. (2023) immersed candidates for biodegradation in deep-sea water that was pumped in situ, thus maintaining representative nutrient concentrations and temperatures. However, pressure was not maintained, which induces a significant bias in microbial communities (see Section 4.1.1 In situ). Immersion of samples in semi-realistic environmental conditions could represent a potential solution for less restrictive laboratory analysis methods, which are currently being developed for application in coastal environments. Ideally, seawater should be directly sampled from the environment of interest in an open circuit, while its environmental characteristics (such as pressure, temperature, absence of UV radiation and nutrients) are maintained. The understanding of biofilm dynamics, in particular competition phenomena, and the resulting selection pressures, is incomplete. Modifying temperature, nutrient concentration or pressure can alter microbial community composition and impact degradation mechanisms. Manipulations should be carried out under conditions which are as sterile as possible to avoid introducing other strains. Such constraints are technically challenging, which is one of the reasons why studies on deep-sea biodegradation are scarce. A deeper understanding of biological aspects is crucial to allow easier methodologies and implementation of biodegradation studies in the laboratory.

Fig. 8. Hyperbaric pressure chamber on mechanical test frame to study mechanical response under pressure, Cartié et al., 2006

A number of studies have been conducted to investigate the biodegradation of conventional polymers (reviewed by Matjašič et al. (2021) and Lv et al. (2024)) and biopolymers (Gonda et al., 2000; Hachisuka et al., 2023; Kasuya et al., 2000; Kato et al., 2019; Sekiguchi et al., 2011b) by specific strains recovered from the deep sea and then cultivated in the laboratory under specific conditions, mainly bacteria but also fungi. These studies have enabled the identification of strains capable of breaking down and mineralising the materials under study. Nevertheless, these studies are insufficient to prove degradation in natural environments, as questions remain concerning interactions, competition and colonisation in biofilms.

5. Conclusion

The biodegradation of polymers in deep-sea environments is of considerable scientific importance. A significant proportion of the plastic litter that reaches the oceans is likely to be transported to the deep sea, potentially resulting in extensive contamination and disruption of these environments. Consequently, an exclusive focus on biodegradation in coastal marine environments is insufficient for the development of materials that are genuinely biodegradable under all marine conditions. It is imperative that the biodegradation of these materials be characterised in deep-sea environments. To date, the available literature on this topic is extremely limited, with only two studies reported. Their results are highly encouraging for the most promising material family, the PHAs. However, other biodegradable biopolyesters in coastal environments have demonstrated minimal to no indications of degradation. Consequently, the applicability of findings from coastal to deep-sea environments is currently uncertain. Therefore, there is a critical need to expand the number of studies conducted in deep-sea environments.

Given the current state of knowledge, studying rigorously the mechanisms of biodegradation in these environments requires substantial technical and human resources. Ex-situ experimentation has not yet reached a level of representativity that would allow for the proof or characterisation of biodegradation in real environments. The limited knowledge of the biology in these environments, of the interactions within biofilms (both in the deep sea and coastal marine environments), and the technical challenges posed by environmental conditions (pressurisation, high distance of operation, high costs) are the main factors that hinder our understanding of these processes. Advances in these three areas could facilitate the democratisation of these experiments and provide invaluable knowledge for two major scientific fields of research. First, for deep-sea biology and the comprehension of the biogeochemical cycles of marine environments, which are deeply involved in the regulation of Earth's climate (which is of urgent importance in a context of climate change) (Boyd et al., 2019; Levin and Le Bris, 2015). Second, for the characterisation of the impact and resolution of extensive anthropogenic pollution currently affecting these environments and therefore these cycles (Ramirez-Llodra, 2020). The viability of these experiments depends on the implementation of mutualisation and collaborative practices. They are highly transdisciplinary and necessitate the utilisation of the most advanced technologies in both biological research and deep-sea experimentation, as well as the allocation of considerable financial resources. This represents a significant challenge, one that is essential if we are to effectively address the issue of plastic pollution in the oceans.

CRediT authorship contribution statement

Alexandre Chamley: Writing – original draft. **Christophe Baley:** Writing – original draft. **Marjolaine Matabos:** Writing – original draft. **Pauline Vannier:** Writing – review & editing. **Pierre Marie Sarradin:** Writing – review & editing. **Floriane Freyermouth:** Writing – review & editing. **Peter Davies:** Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alexandre Chamley reports financial support was provided by Direction Générale de l'Armement. Other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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