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Review

Pressure as an environmental parameter for microbial life — A review

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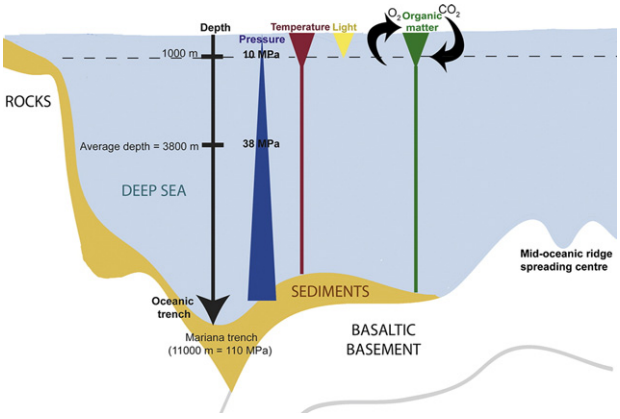
HIGHLIGHTS

- High-pressure environments represent the largest habitat for microbial life on Earth.
- Pressure generally enhances microbial activity rates in deep environments.
- Pressure is potentially a limiting parameter for life at depth.
- The field of high-pressure geomicrobiology is to be expanded.

GRAPHICAL ABSTRACT



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ABSTRACT

Microbial life has been prevailing in the biosphere for the last 3.8 Ga at least. Throughout most of the Earth's history it has experienced a range of pressures; both dynamic pressure when the young Earth was heavily bombarded, and static pressure in subsurface environments that could have served as a refuge and where microbial life nowadays flourishes. In this review, we discuss the extent of high-pressure habitats in early and modern times and provide a short overview of microbial survival under dynamic pressures. We summarize the current knowledge about the impact of microbial activity on biogeochemical cycles under pressures characteristic of the deep subsurface. We evaluate the possibility that pressure can be a limiting parameter for life at depth. Finally, we discuss the open questions and knowledge gaps that exist in the field of high-pressure geomicrobiology.

Contents

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1. Introduction

Here we consider pressure as a thermodynamic parameter (S.I. unit Pascal, Pa) that has been acting on the distribution, activity, survival and death of microorganisms in the environment throughout the Earth's history [1–4]. Nowadays microbial life is potentially present in all of the Earth's surface layers — atmosphere, hydrosphere (oceans, rivers, lakes, water vapor, ice caps, glaciers and aquifers), sediments, and both continental and oceanic crusts [5–7]. Beyond the well-investigated oceanic and continental surface settings, the less accessible deep sea, sub-seafloor and continental subsurface represent the largest habitats by volume on Earth for microorganisms [8]. In these remote dark environments, the most unique physical parameter is pressure *P*. In aquatic settings hydrostatic *P* is caused by the weight of the overlying water column. The seawater level defines the hydrostatic zero level. The hydrostatic pressure gradient depends slightly on the salinity of water and is about 10 MPa km^{-1}. In porous sediments and rocks, lithostatic pressure is caused by hydrostatic pressure and by the overburden weight of material. Deviatoric stress is negligible in the present settings of interest. The increase in lithostatic pressure is of ~15 MPa km^{-1} in sediments and of ~28 MPa km^{-1} in continental and oceanic rocks [9].

As oceans cover 71% of the Earth's surface marine environments are the largest high-pressure habitats for microbial life. The upper limit of the deep sea has been set below the photic zone and the thermocline at 1000 m water depth [10], which also delimits the lower pressure (10 MPa) for the piezosphere [11]. *P* in the deep sea ranges from 10 MPa to 110 MPa at the ocean's deepest location Challenger Deep (11,034 m water depth in the Mariana Trench) with an average of 38 MPa [10]. Pressures higher than 110 MPa can only be reached in the subseafloor that is composed of sediments and mafic and ultramafic rocks [12]. The upper 500 m of igneous oceanic crust is mainly composed of basalts that are porous and host the largest aquifer on Earth (2% of the ocean water volume) [12]. Marine sediments cover much of the oceanic crust with a thickness of 500 m on average that can reach 10 km in some deep-sea trenches [12]. On the continental side, high-pressure habitats comprise various sedimentary, igneous and metamorphic rocks, as well as groundwaters from mines and aquifers [13]. At the present day temperature in the deep ocean is uniformly close to 2–3 °C away from hydrothermal vents [14]. In the lithosphere heat is transferred by conduction. The increase in temperature in the subseafloor and continental subsurface depends on the thermal conductivity of rocks and sediments, and follows an average geothermal gradient of 25 °C km^{-1} [9] except at deep sea hydrothermal vents and hot spring where the heat is transferred by convection. Microbial communities have been studied for more than 20 years in the deep marine sedimentary subseafloor and for even longer in the deep sea [15]. The microbiology of the oceanic rocky environments remains largely unexplored [16–18]. Studies investigating the effect of *P* have been limited to samples originating from seawater, marine sediments and hydrothermal vents. Although the microbiology of the continental subsurface has been explored for as long as the marine subsurface [19], the effects of pressure on microorganisms in these environments remain largely unknown.

In this review, we first consider the effects of dynamic and static pressures on both the origin and survival of microbial life on early Earth (Section 2). In Section 3 we examine the effects of high *P* on (i) microbial growth, (ii) microbial metabolic processes that influence biogeochemical cycles and (iii) microbial survival in deep subsurface environments. We finally discuss the knowledge gaps in the field of high-pressure geomicrobiology in Section 4. The historical background of high-pressure biology has recently been summarized by Demazeau and Rivalain [20]. Pressure-based biotechnological applications such as food processing, disinfection of biomaterials, development of vaccines and protein refolding have also been recently reviewed elsewhere [21–23]. For an overview of the general effects of high *P* on microbial physiology, the reader is referred to other reviews [24,25]. Mentré and Hui Bon Hoa provided an interesting overview of the role of water in the *P* effects on biological macromolecules [26].

2. Pressure as a permanent or transient environmental parameter on early Earth

2.1. Origin of life at high pressure

It has been emphasized that life could actually have arisen at high *P* [2,27] in subsurface environments such as hydrothermal vents or subduction trenches [28–31]. During the Earth infancy in the Hadean and Archean times, continents and a large proto-ocean were already present as testified by the oldest zircons [32,33]. Both the tectonic regime and topography induced by the hot Hadean–Archean mantle were radically different from those at present day [34,35]. As the mantle was a couple hundred degrees hotter than today, water was recycled much more efficiently in subduction zones toward the

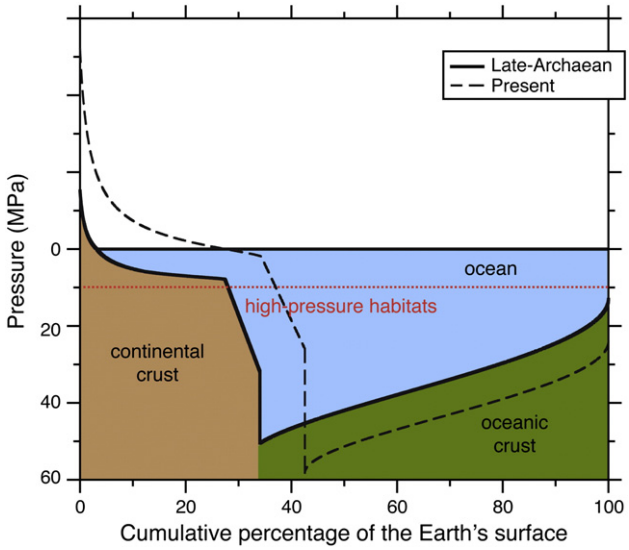

Fig. 1. Comparison of the topography of high-pressure habitats (>10 MPa) on the Archean and modern Earth. The volume of the oceans was larger and the topography between continents and oceanic seafloor was less contrasted in the Archean time (black continuous line) than today (black dotted line).
Courtesy of N. Coltice, adapted from Flament et al. [35].

surface due to a shallower dehydration of the slab and to a larger degassing of the hot magmas. This suggests that the ocean in the early Archean had a much larger extension than at present day and high-pressure habitats (>10 MPa) covered more than 2/3 of the Archean Earth's surface (Fig. 1). The early Ocean flooded the oceanic crust and the margins as today, as well as most of the continental crust unlike at present day [35]. The latter flooded continental crust represented approximately 1/4 of the Earth's surface while the emerged continents less than 1/10. The oceanic seafloor was under slightly lower *P* on average compared to the mean present day value of 38 MPa. The flooded continent surface was under a moderate average *P* of 7 MPa [35]. The oceanic crust was produced by a higher degree of partial melting from the hot mantle, and it could be about 20 km thick, i.e. 3 times the modern one (7 km), and it could also be overloaded by large amounts of magmatic products from hot spots [34]. As the young continental crust was enriched in short-lived radioactive elements and therefore hot, it was less viscous [34]. Serpentinization of the ultramafic seafloor (komatiites) could have generated a flux of molecular hydrogen in the Hadean approximately 7 to 8 orders of magnitude larger than at present day [36] and could have supported the development of life like at hydrothermal vents [37]. The Hadean eon was punctuated by warm or maybe Inferno episodes during the late-stage bombardment. Tens of 10 to 100-km size asteroids might have statistically hit the Earth ~3.9 Ga ago, at the time life could have been emerging. As a matter of fact, the oldest traces of life date from 3.8 Ga ago and are preserved as heavy carbon isotopic signatures in the sedimentary rocks from Isua [38]. However, the habitable zone was certainly never fully sterilized on Earth [39], at least since the termination of primary accretion of the planets and the postulated impact origin of the Moon 4.5 Ga ago [40]. This might have favored high-temperature habitats suitable to hyperthermophilic and thermophilic microorganisms, while mesophilic habitats would still be present [39]. This suggests that the deep subsurface habitats under high hydrostatic *P* may have protected emerging life from the late heavy bombardment, from harmful radiations and buffered physico-chemical variations, and therefore provided a more stable environment propitious for the emergence of life from pre-biotic chemistry and/or the preservation of existing life.

2.2. Microbial life submitted to dynamic pressure

At the surface of the early Earth, microbial life was submitted to dynamic *P*, i.e. a brief *P* rise associated with elevated temperature, during meteoritic impacts. The effects on microorganisms of short pulses of elevated *P* and associated increase in temperature have hardly been investigated. Shock experiments usually seek to test the hypothesis of lithopanspermia — the potential transfer of microbial life from a planet to another through rock fragments ejected as a consequence of meteoritic impacts [41] — but also inform on whether microorganisms would have survived on a bombarded planet. A few shock studies have shown that microorganisms survived shocks induced by low-velocity impactors (e.g. from Mars) at the surface of the Earth and that survival was quite variable from one microorganism to another (Table 1) [42–47]. The geological material that is used to embed microorganisms for the shock experiment also had an influence on the survival rate [42,43]. Studies have been conducted using the shock reverberation technique or the two-stage light-gas gun that produce up to peak pressures of ~80 GPa for less than 1 μs associated to a brief and intense increase in temperature. For instance, with the shock reverberation technique, a *P* peak of 30–34 GPa corresponds also to a peak temperature of 390 °C for less than 0.3 μs, followed by post-shock temperatures of 220–275 °C for several minutes. Nevertheless viable spores of *Bacillus subtilis* were recovered after the shock treatment [46]. Spores of *B. subtilis* and the lichen *Xanthoria elegans* survived up shock pressures of up to ~45 GPa, whereas the cyanobacterium *Chroococcidiopsis* sp. does not survive shock >10 GPa [42–45], while other investigators claim that *Rhodococcus erythropolis* and *B. subtilis* cells survive up to ~78 GPa [47]. Most shock studies have only investigated microbial survival after simulated low-velocity meteoritic impacts typical of those that occurred on the young Earth. Investigations of shock-induced chemical and/or structural transformations occurring at the cellular level would certainly improve the understanding of the early evolution of life on earth.

3. Pressure as an environmental parameter in subsurface environments on modern Earth

3.1. Static pressure in deep environments — generalities

The general purpose of studying subsurface environments is to delimit the physical boundaries for microorganisms to live and influence biogeochemical cycles. Access to the deep subsurface is restricted due to technical constraints, and the recognition of the role of the "deep biosphere" in biogeochemical cycles is relatively recent [5]. The data collected over the last two decades have provided estimations of the total microbial biomass in subseafloor sedimentary environments from coastal areas to the most oligotrophic oceanic gyres [6,48–50]. Although estimates of the total carbon in the subseafloor vary greatly from 4 to 303 Gt C, microorganisms living in deep subsurface environments are alive and have developed metabolic strategies to cope with severe energy limitation [51]. The limits for life at depth are not established yet. At first glimpse, nutrient availability and temperature appear as the main parameters driving life distribution and diversity at depth [5,52,53]. However, while overcoming technical difficulties, it is being more and more recognized that *P* is also a parameter that controls life distribution and activity in the subsurface [11,12,54–56]. In this section we explore the effects of pressure on (i) growth, or biomass production, (ii) microbial activity, referring to the energy-yielding metabolic processes that affect biogeochemical cycles, and on (iii) survival, which is commonly measured as colony-forming ability. For anabolic processes being more sensitive to pressure

Table 1
Summary of the literature investigating the effects of dynamic pressure on microbial survival.

Microorganism	Matrix	Peak pressure (GPa)	Survival rate (%)	Reference
Bacillus subtilis (spores)	Quartz crystal disk	32	0.01–0.0006	[46]
Bacillus subtilis (cells)	Porous ceramic projectile	78	0.004	[47]
Bacillus subtilis (spores)			0.002	
Rhodococcus erythropolis			0.000008	
Bacillus subtilis (spores)	Gabbro	42	0.01	[44]
Xanthoria elegans		42	0.01	[45]
Chroococcidiopsis sp.		10	0.1	
Bacillus subtilis (spores)	Gabbro, dunite, sandstone, artificial regolith, halite	27–32.5	0.04–0.5	[43]
		42	0.02–0.06	
Bacillus subtilis (spores)	Gabbro, dunite, sandstone, artificial regolith, halite	50	0.01	[42]
Xanthoria elegans		41	0.02–0.9	
Chroococcidiopsis sp.		10	0.02–0.03	

than catabolic processes, the pressure range for activity and survival is much larger than the pressure range for growth [57–60].

3.2. Definition of pressure adaptation

The importance of high *P* as an environmental parameter for microorganisms was first acknowledged by Certes in 1884 while working on microorganisms isolated from deep-sea sediments recovered at 5000–6000 m water depth during the Travailleur and Talisman expeditions (1882–1883). At that time Certes already questioned the participation of microorganisms in the transformation of organic matter in the deep sea [61] and showed that microorganisms can actually thrive under high hydrostatic *P* [62]. More than half a century later, the influence of hydrostatic *P* on microbial growth in terrestrial and marine bacteria was recognized [63,64]. Those who grow better at high hydrostatic *P* were called "barophilic" in these early days [64]. Yayanos demonstrated the existence of barophilic microorganisms with the isolation of the first pressure-adapted bacterium [65] and renamed "piezophilic" the microorganisms that have a higher growth rate at high hydrostatic *P* [1]. He also determined that piezophilic isolates originate from deeper than 2000 m water depth and that isolates showing obligate piezophily only came from below 6000 m water depth [66]. Only a few tens of piezophilic isolates have been characterized over the last decades (see the most recent inventory in [11,67]), mainly from deep-sea sediments and animals, and hydrothermal vents (Fig. 2). The optimum temperature of piezophilic isolates is consistent with their origin. Piezophilic isolates from sediments and animals are psychrophilic to mesophilic while piezophilic isolates from hydrothermal vents are mesophilic to hyperthermophilic. All psychrophilic to mesophilic isolates are found in the domain of Bacteria. Until recently they were restricted to the genera *Shewanella*, *Psychromonas*, *Colwellia*, *Moritella* and *Photobacterium* [67,68], as isolation procedures usually involved high nutrient concentrations. The improvement of isolation techniques using natural concentrations of nutrients [67] has led to the isolation of three sulfate-reducing strains of *Desulfovibrio* [69–71], one strain of *Carnobacterium* [72] and one strain of *Rhodobacterales* bacterium [67] characterized as piezophiles. Thermophilic and hyperthermophilic isolates are taxonomically more diverse as hydrothermal vent microorganisms might be less affected by nutrient-rich isolation procedures. They are found in the domain of Archaea, except for three thermophilic bacterial isolates [11]. The existence of piezophilic hyperthermophilic Archaea is consistent with the hypothesis of origin of life under pressure in a warm environment, such as hydrothermal vents [30]. However these scarce isolates are probably not representative of the diversity of the piezophilic populations found in high-pressure environments. The latter observation is likely explained by the use of rich isolation media and/or by the unavoidable decompression that occurs during the different steps of enrichment and isolation of microbial isolates. Thus far, only two studies have reported collection and isolation of microorganisms from seawater [73] and gas-hydrate sediments [74] without decompression. Unfortunately, these strategies did not result in the expected isolation of obligate piezophiles. It is generally assumed that as long as samples from the deep sea are maintained at low temperature [75], a limited number of decompression and compression cycles are not critical for the recovery of obligate piezophilic isolates [76]. Extensive studies of few piezophilic deep-sea bacteria (e.g. *Photobacterium profundum* SS9 or *Shewanella violacea* DSS12) have provided clues about the genomic and physiological adaptations that allow them to grow faster at high *P* [3,25,77–79]. Piezophilic and piezosensitive *Pyrococcus* species have different sequences in orthologous proteins, stressing the existence of piezophilic amino acids [80,81]. In comparison the effects of high *P* on microbial energy-yielding metabolic processes have hardly been investigated.

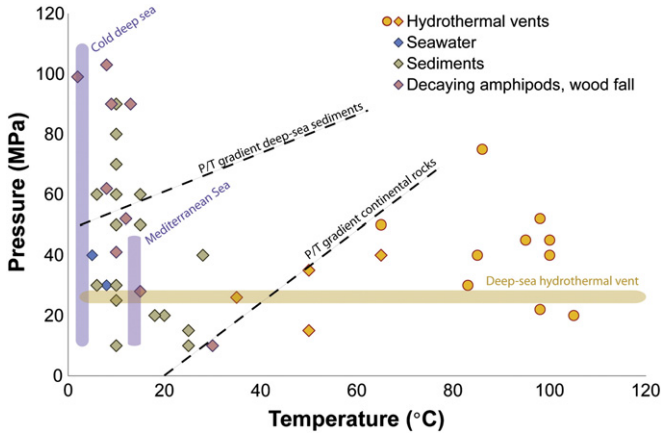

Fig. 2. Optimal pressure (P) and temperature (T) conditions for growth of described piezotolerant and piezophilic isolates. Bacteria (triangles) and Archaea (circles) are plotted as a function of origin, hydrothermal vents (yellow), seawater (blue), sediments (gray) and decaying amphipods and wood fall (pink).
P/T data for optimal growth were extracted from Fang et al. [11] and Eloe et al. [67]. Figure inspired by Fig. 1 in the review of Yayanos [1].

3.3. Influence of pressure on microbial activities relevant to deep biogeochemical cycles

Microorganisms are key players in biogeochemical cycles not only at the surface of the Earth but also at depth in the upper lithosphere [5]. Primary production by phototrophic microorganisms at the surface of the oceans accounts for about half of the planet's primary production [82]. In the oceans, organic carbon is available to microorganisms as particulate organic carbon (POC) and dissolved organic carbon (DOC). Heterotrophic microorganisms degrade and remineralize most of the organic matter below the photic zone using oxygen as an electron acceptor [83] and only 1% of the organic matter produced at the surface reaches the seafloor at water depths of 5000–6000 m [10]. After oxygen has been depleted, usually in the first mm to cm of the subseafloor sediments, oxidation of organic matter continues under anoxic conditions using a sequence of electron acceptors [15]. In the past few years, the subseafloor sediments of the most oligotrophic regions of the world's ocean have been shown to be oxic up to several meters below the seafloor, resulting in microbial aerobic degradation of organic matter deep in the sediments [84–87]. Pressure effects on microbial aerobic and anaerobic activities relevant to biogeochemical cycles have been investigated in natural samples and in pure cultures (Fig. 3). Studies using natural samples examined activity rates at/near in situ pressure of collection and compared them to activity rates measured at atmospheric pressure. Studies of pure cultures explored a larger range of pressures to infer the pressure limits of metabolic process. Unfortunately the latter approach is difficult to perform with natural samples, usually because the number of samples and/or pressure vessels is limited. In this review, we complement the recent review on the effects of pressure on microbial activity in oxic oceanic waters by Tamburini et al. [56] with a summary of the effects of pressure on aerobic and anaerobic processes in deep-subseafloor sediments and at hydrothermal vents (Table 2).

According to the Le Chatelier's Principle, a pressure increase favors chemical reactions that occur with reduction in system volume. However given the complexity and variability of metabolic pathways, it is difficult to predict how *P* will affect metabolic rates in the environment [11,88], it is therefore crucial to perform experimental and field studies as shown below. Pressure inhibits aerobic heterotrophic microbial activities in surface seawater (<200 m) — hydrolytic enzymatic activities (e.g. aminopeptidase, phosphatase…), carbon uptake, respiration and biomass production (as measured by thymidine and leucine incorporation) — in the Mediterranean Sea [89–93], in the

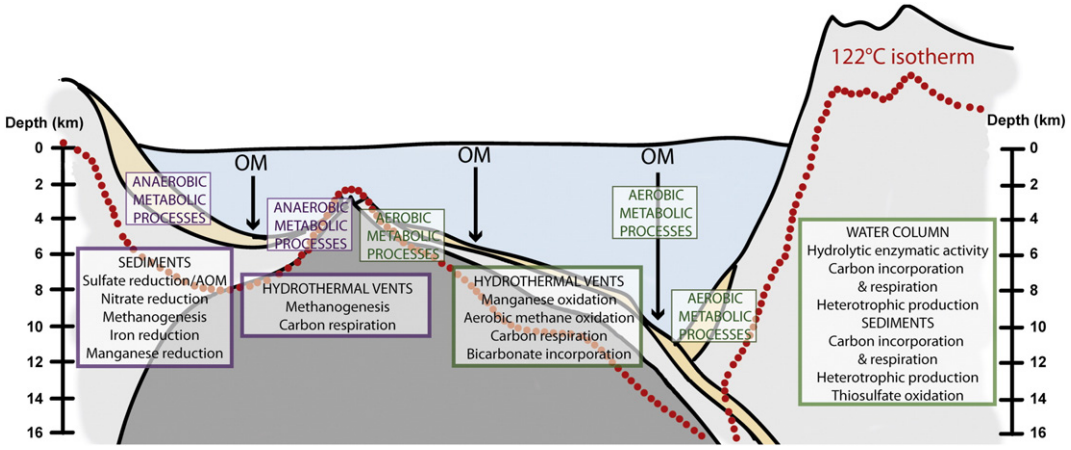

Fig. 3. Deep-subsurface microbial metabolic processes studied at high pressure. The 122 °C isotherm delimits the potential temperature limit for life.

Atlantic Ocean [94–104] and in the Strait of Georgia (Pacific) [105]. This suggests that most of the organic matter escaping the photic zone might eventually reach the seafloor sediments [97]. Pressure has generally a positive effect on microbial activities in oxic conditions in the deep sea, as shown in seawater samples from the Mediterranean Sea [89–91,106–108] and in seawater, sediment samples, animals, and isolates from the Atlantic [98,109–120] and Pacific [104,105] oceans. Oppositely, a few investigations reported the lack of significant pressure effect on microbial activity [121–123] and the early studies showed a negative effect of pressure on microbial activities (carbon incorporation and respiration) in seawater and surface sediments, as well as isolates [73,95,100,101,103,110,111,124–128,145]. It is plausible that the latter results were biased by very high substrate concentrations and that may have inhibited microbial activities at high pressure [10,113]. Decompression thus seems to have a great impact on the metabolic potential of subsurface microorganisms. As a consequence, measuring microbial activity in the deep ocean and respiration rates in particular at atmospheric *P* will generally lead to an underestimation of the rates of transformations of organic carbon and will minimize current estimates of global fluxes of carbon in the ocean [56].

The few aerobic processes investigated at hydrothermal vents, are enhanced by high *P* [129–133]. Fewer studies are available on anoxic processes occurring in subseafloor and hydrothermal environments at high *P*, and most of them used pure cultures (Table 2). Sulfate reduction coupled to anaerobic oxidation of methane (AOM) or to organic matter oxidation, methanogenesis, organic carbon respiration (coupled to elemental sulfur reduction), iron reduction, manganese reduction and nitrate reduction are stimulated at high *P* (Table 2) [129,134–143]. The isolation of piezophilic sulfate-reducing bacteria and methanogens [11] confirms that enhanced sulfate reduction and methanogenesis at high *P* in deep environments is mainly caused by piezophilic microorganisms [135–138]. However, it was recently shown that rates of Fe(III) reduction by piezosensitive *S. oneidendis* MR-1 are enhanced up to 40 MPa, suggesting that piezosensitive isolates might also contribute to deep biogeochemical cycles [139]. Although it is not yet possible to sample sediments without decompression on a regular basis, a recent study has shown that high *P* storage, until microbial activity is measured, maintained active piezophilic sulfate-reducing communities [138]. This importance of storage at in situ *P* has also been highlighted in a study of deep oxic sediments of the Atlantic Ocean [119]. To date the studies showing a positive effect of pressure on sulfate reduction in isolates from oil well brines and on nitrate reduction in groundwater from an aquifer are the only studies looking at the effect of pressure in continental subsurface environments [64,144].

Microbial activity occurs over a larger range of *P* compared to growth, as shown for pure cultures in anoxic conditions [134,139,140]. In natural samples in oxic conditions, increased *P* induces a greater proportion of total organic carbon to be respired than incorporated (e.g. [95,125,126,128,145]), suggesting that energy-yielding processes are less sensitive to *P* than biomass production. A link between the *P* range for activity and for survival is expected. In cultures of *S. oneidensis* MR-1 the pressure range for Fe(III)-reducing activity was correlated with the colony-forming ability [139]. However this link is difficult to evaluate in natural samples, as viability or colony-forming ability of deep microbial communities is not measurable using classical microbiological techniques. In the next paragraph, we will evaluate the effects of pressure on viability, as measured by colony-forming ability, of relevant microbial cultures.

3.4. Microbial death in the deep subsurface — is pressure a limit for life?

Since the 1990s the food industry has increasingly used high *P* for inactivating pathogenic microorganisms while preserving the food nutritional and organoleptic properties. Many studies have thus investigated microbial inactivation, defined as the loss of colony-forming ability, between 100 and 1200 MPa over a large range of temperatures including sub-zero temperatures [146]. Vegetative bacteria are generally inactivated in the range of 200–600 MPa while spores require much higher pressures in the range of 1200–1500 MPa. As experimental conditions in food processing are significantly different from environmental conditions, it is thus difficult to know whether the pressure limits for survival could also apply in the environment. The current understanding derived from the few studies simulating environmental conditions is that the viability of piezosensitive microorganisms is severely decreased at *P* ~100–150 MPa [57–59,139,147,148]. As a consequence, pressure might be a limit for microbial survival in the deep continental subsurface or deep in the subseafloor, but not in the deep sea. As the temperature limit for life is currently at 122 °C, as measured in pure cultures [142], temperature might be the first limiting parameter in subsurface environments except at subduction zones, where the temperature gradient is low [52]. Both piezosensitive and piezophilic microorganisms have been isolated at Challenger Deep, the oceans' deepest location in the Mariana Trench which is at a pressure of ~110 MPa and at a temperature of 2 °C [76,149,150]. Microbial carbon turnover rates are relatively high at Challenger Deep suggesting that microbial cells are alive and active at that pressure [151]. Live microbial cells have also been detected at *P* as high as ~78 MPa in the deep subseafloor sediments of the Newfoundland margin at a temperature of 60–100 °C and a depth of 1613 mbsf under a water column of 4570 mbsl [152]. The most piezophilic microorganism (*Moritella yayanosii* MT-41) was isolated from the Mariana Trench and is able to grow up to 130 MPa [76]. It might be able to subsist at even higher pressure, however the effects of pressure on survival in piezophilic isolates have not been investigated.

Table 2
Survey of the literature investigating the effects of pressure on microbial activities in natural samples or pure cultures relevant for biogeochemical cycles. Total uptake corresponds to respiration + incorporation into cells.

Metabolic activity monitored	Sample	Origin of sample	Depth of origin (m)	Incubation *P* (MPa)	*P* effect	Reference
Aerobic metabolic processes – ocean surface samples						
Mediterranean Sea						
^{14}C-glucose incorporation	Seawater	NW Mediterranean Sea	20	11	−	[91]
^{14}C-glucose incorporation	Seawater	NW Mediterranean Sea	20	11	−	[90]
^{14}C-glucose total uptake	Seawater	NW Mediterranean Sea	20	11	−	[89]
Aminopeptidase activity Silicic acid dissolution	Seawater+culture of diatom *Thalassiosira weissflogii*	NW Mediterranean Sea	200	Up to 14	−	[93]
Organic matter degradation	Filtered seawater amended with particles (from trap)	NW Mediterranean Sea	200	Up to 15	−	[92]
Atlantic Ocean						
^{14}C-acetate total uptake ^{14}C-mannitol total uptake ^{14}C-glutamate total uptake ^{14}C-amino acids total uptake	Seawater	NW Atlantic Ocean (34°0'N, 69°59'E)	200	53	−	[94]
^{14}C-acetate total uptake ^{14}C-mannitol total uptake ^{14}C-glutamate total uptake ^{14}C-amino acids total uptake	Seawater	NW Atlantic Ocean	200	18	−	[100]
^{14}C-glutamate total uptake ^{14}C-amino acids total uptake	Isolate (seawater)	NW Atlantic Ocean (Woods Hole)	Surface	5, 20, 40	−	[101]
^{14}C-glutamate total uptake Oxygen consumption	Isolate EP-4 (seawater)	NW Atlantic Ocean (Woods Hole)	Surface	50	−	[102]
^{14}C-glutamate total uptake	Seawater	NW Atlantic Ocean (Woods Hole)	Surface	19	−	[95]
Thiosulfate oxidation	Seawater	NW Atlantic Ocean (34°0'N, 69°59'E)	200	53	−	[103]
Sugar uptake Sugar phosphorylation	*Vibrio marinus* MP1		Surface	0–100	+ (<20) − (>20)	[104]
^{3}H-leucine incorporation ^{3}H-thymidine incorporation	Seawater	NE Atlantic Ocean	10, 40	10, 20, 30, 43	−	[97]
^{3}H-leucine incorporation ^{3}H-thymidine incorporation	Particles (trap)	NE Atlantic Ocean	200	10, 20, 30, 43	−	[97]
^{3}H-leucine incorporation ^{3}H-thymidine incorporation	Seawater	NE Atlantic Ocean (Goban Spur)	14, 153	15, 30, 45	−	[98]
^{3}H-leucine incorporation ^{3}H-thymidine incorporation	Seawater	NE Atlantic Ocean (King Arthur Canyon)	10, 13, 54, 150	15, 30, 45	−	[98]
^{3}H-leucine incorporation ^{3}H-thymidine incorporation	Seawater	NE Atlantic Ocean (Porcupine Abyssal Plain)	150	45	−	[99]
^{3}H-thymidine incorporation	Seawater	E Atlantic Ocean (Cape Verde Plateau)	154	45	−	[99]
Oxygen consumption	Organo-mineral aggregates	NE Atlantic Ocean (Lisbon Canyon)	367	10, 20, 30	−	[96]
Oxygen consumption	Organo-mineral aggregates	NE Atlantic Ocean (Nazare Canyon)	301	10, 20, 30	−	[96]
Oxygen consumption	Artificial aggregates	Mixture of algae	Surface	10, 20, 30	−	[96]
Pacific Ocean						
^{14}C-glucose incorporation	Seawater	Pacific Ocean (Strait of Georgia)	Surface	2, 4	−	[105]
Aerobic metabolic processes – deep-sea samples						
Mediterranean Sea						
^{14}C-glucose incorporation	Seawater[a]	NW Mediterranean Sea	1100	11	+	[91]
^{14}C-glucose incorporation	Seawater[a]	NW Mediterranean Sea	1100	11	+	[90]
^{14}C-glucose total uptake ^{14}C-amino acid total uptake ^{3}H-thymidine incorporation	Seawater[a]	NW Mediterranean Sea	800 1000 1150 1500 2000	8 10 11.5 15 20	+	[89]
Phosphatase activity Aminopeptidase activity ^{3}H-leucine incorporation	Seawater[a]	NM Mediterranean Sea	1000 1500 2000	10 15 20	+	[106]
Aminopeptidase activity ^{14}C-glutamate total uptake	Seawater[a]	NW Mediterranean Sea	1000 1500 2000	10 15 20	+	[107]
Phosphatase activity Aminopeptidase activity ^{3}H-leucine incorporation $^{14}CO_2$ fixation	Seawater[a]	W Mediterranean Sea	2500	25	+	[108]

(continued on next page)

Table 2 (*continued*)

Metabolic activity monitored	Sample	Origin of sample	Depth of origin (m)	Incubation *P* (MPa)	*P* effect	Reference
Atlantic Ocean						
^{14}C-acetate total uptake	Seawater contact water[a]	NW Atlantic Ocean	1830	18	−	[100]
^{14}C-mannitol total uptake	Particles (sediment)[a]					
^{14}C-glutamate total uptake						
^{14}C-amino acids total uptake						
^{14}C-amino acids total uptake	Seawater[a]	NW Atlantic Ocean	1800	12	−	[124]
^{14}C-amino acids total uptake	Isolates (seawater)	N Atlantic Ocean	450	5, 20, 40	−	[101]
^{14}C-glutamate total uptake			1000			
			1550			
			2600			
^{14}C-amino acids total uptake	Sediments	NW Atlantic Ocean	7750	77.5	−	[126]
^{14}C-glutamate total uptake		(Puerto Rican Trench)	8130	81.5		
^{14}C-leucine total uptake						
^{14}C-alanine total uptake						
^{14}C-glutamate total uptake	Seawater[a]	NW Atlantic Ocean	1800	18	−	[95]
		(Bermuda Transect Station)	3000	30		
^{14}C-amino acids total uptake	Seawater[a]	N Atlantic Ocean	1700	17	−	[95]
		(Deep Ocean Station 2)	3130	31.3		
Thiosulfate oxidation	Isolate 12 W	N Atlantic Ocean	4000	53	−	[103]
	Isolate 38 CH (sediment)		4000			
	Isolate 9341 (seawater)		3000			
^{14}C-amino acids total uptake	Seawater[a]	N Atlantic Ocean	2600	26	−	[127]
		(Deep Ocean Station 2)				
^{14}C-glutamate total uptake	Seawater[a]	NW Atlantic Ocean	3550	35	+	[109]
^{14}C-acetate total uptake						
^{14}C-glutamate total uptake	Seawater[a]	SE Atlantic Ocean	5220 & 5225	52	+	[109]
^{14}C-acetate total uptake		(Cape Basin)				
^{14}C-glutamate total uptake	Seawater[a]	SE Atlantic Ocean	5200 & 5220	52	+	[109]
^{14}C-acetate total uptake		(Angola Basin)				
^{14}C-acetate total uptake	Strain C-5[a]	NW Atlantic Ocean	4000	40	−	[73]
		(Bermuda Rise)				
^{14}C-glutamate total uptake	Seawater[a]	NW Atlantic Ocean	1800–3060	18–30.6	−	[111]
^{14}C-amino acids total uptake			1700–3500	17–35	−	
^{14}C-acetate total uptake			1750–4620	17.5–46.2	−/=	
^{14}C-glucose total uptake			1830–6000	18.3–60	−/+	
^{14}C-glutamate total uptake	Sediment	NW Atlantic Ocean	3600	36	+	[110]
^{14}C-acetate total uptake						
^{14}C-glutamate total uptake	Sediment	SE Atlantic Ocean	5200	52	=	[110]
^{14}C-acetate total uptake		(Cape Basin)				
^{14}C-glutamate total uptake	Sediment	SE Atlantic Ocean	5200	52	=	[110]
^{14}C-acetate total uptake		(Angola Basin)				
^{14}C-glutamate total uptake	Sediment	SE Atlantic Ocean	4300	43	=	[110]
^{14}C-acetate total uptake		(Walvis Ridge)				
^{14}C-glutamate total uptake	Amphipods	NW Atlantic Ocean	3600	36	−	[110]
^{14}C-acetate total uptake						
^{14}C-glutamate total uptake	Fish & amphipods	SE Atlantic Ocean	5200	52	+/−	[110]
^{14}C-acetate total uptake		(Cape Basin)				
^{14}C-glutamate total uptake	Amphipods	SE Atlantic Ocean	5200	52	−	[110]
^{14}C-acetate total uptake		(Angola Basin)				
^{14}C-glutamate total uptake	Holothurians	SE Atlantic Ocean	4300	43	+	[110]
^{14}C-acetate total uptake		(Walvis Ridge)				
^{14}C-glutamate total uptake	Holothurian & sediment	NW Atlantic Ocean	4430	44	+	[112]
		(Demerara Abyssal Plain)				
^{14}C-glutamate total uptake	Sediments	NW Atlantic Ocean	4470	44.6	+	[113]
	Sinking particles (traps)	(Demerara Abyssal Plain)	4850	48.6		
^{14}C-glutamate total uptake	Sediments	NE Atlantic Ocean	4200	42	+	[114]
		(Bay of Biscay)	4715	47		
Chitinase synthesis	Isolates	South Atlantic Ocean	29–910, 2270,	40	−	[120]
	(sediments, animal guts)	(Bransfield Strait)	4102			
Chitinase activity	Isolates	South Atlantic Ocean	29–910, 2270,	20, 50, 100	+/−	[120]
	(sediments, animal guts)	(Bransfield Strait)	4102			
Organic carbon respiration	Seawater amended with mixture of phytoplankton and zooplankton (10 m)	Mid-North Atlantic Ocean	4585	46	+	[115]
^{3}H-leucine incorporation	Seawater	NE Atlantic Ocean	1509–4416	15, 30, 45	+	[98]
^{3}H-thymidine incorporation		(Goban Spur)				
^{3}H-leucine incorporation	Seawater	NE Atlantic Ocean	1812–3657	15, 30, 45	+	[98]
^{3}H-thymidine incorporation		(King Arthur Canyon)				
^{14}C-labeled algae respiration	Sediments	NE Atlantic Ocean	4550	15, 30, 46	+	[116]
		(BIOTRANS station)				
^{14}C-labeled Cyanobacteria respiration	Sediments	Norwegian Sognefjord	1260	12.8	−	[123]
Hydrolytic enzyme activity						
Hydrolytic enzyme activity	Sediments	NE Atlantic Ocean	2879	29	=	[121]
		(West European Basin	4565	46		
		& Iceland Basin)	4919	50		

Table 2 (*continued*)

Metabolic activity monitored	Sample	Origin of sample	Depth of origin (m)	Incubation *P* (MPa)	*P* effect	Reference
^{3}H-thymidine incorporation	Sediments	NE Atlantic Ocean (Goban Spur)	135, 580, 1252, 1680	1.4, 5.9, 12.7, 17	=	[122]
^{3}H-leucine incorporation	Sediments	NE Atlantic Ocean	4850	49	+	[117]
^{3}H-thymidine incorporation	Sediment contact seawater	(Porcupine Abyssal Plain)				
^{3}H-thymidine incorporation	Sediments	NW Atlantic Ocean	767, 987, 1828,	7, 10, 18,	+/−	[118]
^{14}C-amino acids respiration		(Gulf of Mexico)	2700, 3410, 3535	27, 34, 36		
^{14}C-acetate respiration	Sediments	N Atlantic Ocean	4480	45	+ (storage HP)	[119]
^{14}C-glucose respiration		(North Pond)	4143	45		
			4250	40		
Pacific Ocean						
^{14}C-glucose incorporation	Seawater	Pacific Ocean (Strait of Georgia)	400	4	+	[105]
^{14}C-glutamate total uptake	*Vibrio* MP-38	Pacific Ocean	?	0–50	−	[128]
^{14}C-glycine total uptake		Station NH-4				
^{14}C-phenylalanine total uptake						
^{14}C-proline total uptake						
^{14}C-starch total uptake	Enrichment culture of deep-sea amphipods	N Pacific Ocean (Aleutian Trench)	7050	75	=	[145]
^{14}C-starch total uptake	Sediments & seawater	NW Pacific Ocean (Ryuku Trench)	7000+	75	−	[145]
Sugar uptake	Isolate PE-36	California Coast	3584	0–100	+ (<80)	[104]
	Isolate CNPT-3	North Pacific Ocean	5800	0–100	− (>80)	
					−	
Aerobic metabolic processes — hydrothermal vents						
Mn^{2+} oxidation	*Arthrobacter* sp. 37 (Ferromanganese nodule)	Atlantic Ocean	730	0–57	= (<47)	[129]
					− (>47)	
^{14}C-bicarbonate incorporation	Hydrothermal fluid[a] (white smoker)	East Pacific Ridge (21°N site)	2600	26	+	[132]
^{14}C-bicarbonate incorporation	Hydrothermal fluid[a]	East Pacific Ridge	2500	25	+/−	[133]
^{14}C-acetate total uptake		(Galapagos Rift)				
^{14}C-glucose total uptake						
Mn^{2+} binding	Hydrothermal fluid	Hydrothermal plume (Juan de Fuca Ridge)	2000	20	+	[131]
Aerobic methane oxidation	Hydrothermal fluid (Black smoker)	Endeavour segment (Juan de Fuca Ridge)	2200	20.5	+	[130]
Aerobic methane oxidation	Seawater (1 m from black smoker)	Endeavour segment (Juan de Fuca Ridge)	2200	22	+	[130]
Anaerobic metabolic processes — deep-subseafloor sediments						
Nitrate reduction	22 marine strains	Shallow sea	<4000	0–100	+ (<20)	[134]
	8 marine strains	Philippine Trench	7000–10200		− (>40)	
Manganese reduction	*Bacillus* sp. 29	Ferromanganese nodule (Atlantic Ocean)	1700	0–100	− (>20)	[129]
Sulfate reduction	Strain 80-55 (80 mbsf)	Sediment	900	0–27.5	+ (<15)	[135]
	Desulfovibrius profundus strain 500-1 (500 mbsf)	(Japan Sea)			− (>15)	
Sulfate reduction	Hydrothermal sediments	Guaymas Basin	2013	22, 45	+	[136]
Sulfate reduction	Cold-seep sediments	Gulf of Mexico	1000	10	+ (SR)	[137]
AOM		(Mississippi Canyon)			+/= (AOM)	
Sulfate reduction	Cold-seep sediments	California Coast	1000	10	+ (SR)	[137]
AOM		(Monterey Bay)			+/= (AOM)	
Sulfate reduction	Cold-seep sediments	Gulf of Mexico	500	5	+ (SR)	[137]
AOM		(Garden Banks)			+/= (AOM)	
Sulfate reduction	Cold-seep sediments	Japan Trench	6177	50	+	[138]
			5347			
Methanogenesis	Cold-seep sediments	Gulf of Mexico (Mississippi Canyon)	1000	10	+	[137]
Methanogenesis	Cold-seep sediments	California Coast (Monterey Bay)	1000	10	+	[137]
Iron reduction	*Shewanella oneidensis* MR-1	Lake sediments	Surface	0–110	+ (up to 40)	[139]
					− (>40)	
Anaerobic metabolic processes — hydrothermal vents						
Methanogenesis	*Methanocaldococcus jannaschii*	White smoker chimney (East Pacific Rise)	2600	10, 20, 35	+	[141]
Methanogenesis	*Methanocaldococcus jannaschii*	White smoker chimney (East Pacific Rise)	2600	25, 50, 75	+	[140]
Methanogenesis	*Methanopyrus kandleri* 116 (black smoker fluid)	Kairei hydrothermal field (Central Indian Ridge)	2450	20, 40	+	[142]
CO_2 production (from organic matter oxidation coupled to S_0 reduction)	Isolate ES-4	Hydrothermal chimney	2200	25, 50	+	[143]

(*continued on next page*)

Table 2 (*continued*)

Metabolic activity monitored	Sample	Origin of sample	Depth of origin (m)	Incubation *P* (MPa)	*P* effect	Reference
Anaerobic metabolic processes — continental subsurface						
Nitrate reduction	Groundwater	Aquifer	283	0–30	+ (<10)	[144]
Formate oxidation					− (>10)	
Sulfate reduction	Isolates	Oil well brines	nd	40, 60	+	[64]

−, = and + correspond to a negative, neutral and positive pressure effect, respectively, in comparison to the atmospheric pressure.
[a] Corresponds to a sample recovered and incubated at in situ pressure without decompression steps.

In the last decade studies reporting activity and survival in the GPa range have been published. Bacterial metabolic activity was reported up to pressures of 1060 MPa by Sharma et al. [153]. The results and interpretation were immediately questioned as the criterion used to probe microbial activity and viability was formate oxidation, an enzymatic reaction that occurs also with inactivated cells or with the enzyme only. The study did not investigate the viability of the cells after *P* treatment [154]. Also the strain used in their study, *S. oneidensis* MR-1, was recently shown to stop being metabolically active and forming colonies by pressures in the range of 110–150 MPa [139,148]. Therefore the study by Sharma et al. cannot be considered as a proof of microbial life and activity at GPa pressures. More recently a directed evolution study of *E. coli* showed that a sub-population can adapt and survive after being exposed to pressure up to 2 GPa while the main population extinguishes above 0.7 GPa [60]. Interestingly the *P* resistance of wild strains of a model bacterium like *E. coli* is highly variable from one strain to another [155]. Among the large number of parameters that are probably involved in *P* resistance, the presence of a S-layer in the cell envelope or the resistance to oxidative stress appears to be quite efficient for both Bacteria and Archaea [156,157]. This suggests that Archaea which cell envelope contains a ubiquitous S-layer might be favored at high *P* and great depth. Metagenomic and biomarker studies suggest that Archaea are dominant in marine sediments [49,158]. The limit of life due to *P* increase has not been crossed yet in nature while the latest experimental quests have actually moved this limit far in the GPa range, above the current drilling capabilities.

4. Open questions in the field of high-pressure microbiology

The field of high-pressure geomicrobiology is still in its infancy. Three major questions, which are tightly linked to the investigation of the deep biosphere, need to be answered: (i) what is the significance of piezophilic microorganisms? (ii) do piezophilic microorganisms have unique metabolic capabilities? and (iii) how can we overcome the technical constraints related to high-pressure experimentation?

Microbial life is ubiquitous on Earth and has been evidenced in all subsurface rocks that are permeated by a minimal water flow ([13,159], and references therein). While the quantification of the deep subseafloor biomass has been refined over the years [6,50], the biomass present in the basaltic ocean crust and in the deep terrestrial subsurface remains uncertain [13,160]. Molecular studies have revealed novel uncultured lineages of Archaea and Bacteria in the deep subseafloor sediments [161,162] and in the continental subsurface [19] and archaeal groups common to both environments. Since there is no genomic sequence specific to piezophilic microorganisms known to date, except for pressure-regulated operons found solely in piezophilic *Shewanella* [163], it is not possible at the moment to determine the diversity of piezophiles in the environment by molecular approaches. Only cultivation approaches, followed by the characterization of growth rates at high *P*, will detect the presence of piezophiles in a given environment. It is well known that only a small fraction of cells can be isolated from the environment with the current cultivation techniques [164]. As a matter of fact, the spectrum of cultured subsurface isolates is narrower than the diverse lineages of Bacteria and Archaea detected by molecular techniques [161]. The same truth holds for piezophilic isolates, and it is not surprising that the diversity of piezophilic isolates is not matching the diversity revealed by molecular approaches or even by classic isolation procedures. For example, while Archaea might be dominating subseafloor sedimentary environments [49,158], only piezophilic Bacteria have been isolated from the cold deep sea or from subseafloor sediments ([67], and references therein). As a consequence the relative abundance of piezophilic vs piezosensitive microorganisms in deep environments cannot be assessed yet. Despite the difficulty to cultivate isolates from deep subsurface environments, cultivation studies have succeeded [165–168]. It would be interesting to complement the classical characterization of deep isolates with the measurement of growth rates at high *P*. Finally physiological studies are definitely needed to investigate the metabolic potential, the activity rates and the survival of piezophilic isolates over a large range of *P*.

In the deep subsurface, the pace of life appears to be extremely slow in most environments, with cells that last on timescales of thousands to millions of years [51,84,169]. However those cells whether dormant or adapted for extraordinarily low metabolic activity appear to recover activity rapidly when provided with nutrients in the lab [170]. They also appear to be quite active wherever high thermochemical gradients. If they were dormant spore-like cells, their survivability could actually be quite high under high *P*. The relative contribution of a larger but metabolically slow biomass vs. smaller active communities at geochemical interfaces to the subsurface biogeochemical cycles of H_2, Fe, S, N and C remains a challenge for the next decade. Enhanced metabolic activity in natural environments (seawater and sediments) is generally attributed to the presence of piezophilic microorganisms (e.g. [130,136,138]). Although increasing *P* seems to inhibit the activity of aerobic surface microorganisms (Section 3.3), we reported that anaerobic processes are enhanced at moderate pressures in the piezosensitive *Shewanella oneidensis* MR-1 [139]. The significance of both piezosensitive and piezophilic microbes for biogeochemical cycles at depth remains to be characterized.

As illustrated by studies on microbial activity at high *P* (Section 3.3), deep samples should be collected without decompression. A tremendous effort has been made over the last years for developing in situ subseafloor observatories, new in situ equipment to measure activity directly at the seafloor and high *P* samplers that can maintain high *P* conditions and transfer sample to high-pressure incubators without decompression [see 54,56, and references therein]. However the deep subsurface marine and continental environments remain difficult to access and high-pressure sampling for the deep sea and the subseafloor is not affordable in most cases. Also the recovery of rocky samples at high pressure does not seem possible at the moment. Two recent studies have shown that recompressing sediment samples after recovery from ~5000 to 6000 m water depth and storage under *P* may allow maintaining the activity potential of subseafloor sediment communities [119,138]. Systematic storage under *P* would require a battery of *P* vessels, therefore an internationally coordinated effort could help preserving and sharing sediment material preserved at high *P*. As for the continental subsurface, the development of subsurface laboratories as well as access to deep mines will provide more opportunities to sample

the deep underground. High pressure definitely matters and should therefore be integrated as an essential component of deep biosphere investigations.

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