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The upper temperature limit of life under high hydrostatic pressure in the deep biosphere

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ABSTRACT

High hydrostatic pressure (HHP) is a common factor in the deep sea and provides an ignorable parameter of consideration in all studies related to deep life. High-temperature environments in the deep sea, mainly including hydrothermal vents and deep sediments in the subseafloor, support enormous amounts of biomass, productivity, and diversity of life. Many microbes living there are usually (hyper)thermophilic piezophiles, which cope with the dual stresses of high temperature and HHP at the same time and playing significant roles in geochemical elemental cycling. Knowledge of the upper temperature limit of life under deep-sea HHP conditions can help us to estimate the boundary of the biosphere and explore its habitability on Earth and in extraterrestrial areas, but uncertainties remain. Here, we have summarized the current known knowledge of physiological correlations between high temperature and HHP, as well as the effects of HHP on cells at high temperature. These effects mainly comprise two aspects: biological integrity and metabolic feasibility. The former has been investigated in many studies on various microorganisms, from which we can draw a general conclusion that HHP helps cells maintain biological integrity under high temperature. For the latter, existing studies have provided clues suggesting that both high temperature and HHP challenge metabolic feasibility, but it is still difficult to draw conclusions on the additive effects on metabolism due to the lack of systematic analysis. Here, we also propose a series of questions for further investigation and called for more attention on metabolic responses to high temperature and HHP; this could provide a direct bridge between geochemistry and ecology, help us to understand the microbial functions in the deep biosphere and allow us to estimate the boundaries of life and habitats.

1. Introduction

1.1. High hydrostatic pressure (HHP) is a common factor in the deep sea

Oceans cover more than 70% of the Earth's surface area, and microbes comprise approximately 90% of the ocean biomass; they are regarded as an important hidden driver of essential elemental cycling (e.g., C, N, S) in the ocean (Karl 2007; Sunagawa and Salazar 2017; Sephton et al., 2018). The deep sea refers to water depths greater than 1000 m. As the hydrostatic pressure increases by approximately 0.1 MPa for every 10 m increase in water depth, the hydrostatic pressure in the deep-sea is higher than 10 MPa. While in sediments, the pressure increases 15 MPa per kilometer (Cario et al., 2019). The average depth of oceans is 3800 m, which provides an average hydrostatic pressure of approximately 38 MPa (Jannasch and Taylor 1984). Hydrostatic pressure influences the physiology of organisms living in the deep sea, which is the largest habitat of the biosphere in terms of volume (1.3×10^{18} m^3) (Whitman et al., 1998). In general, deep-sea prokaryotes are known to be predominantly piezophilic, that means adapted to high-hydrostatic pressure conditions (Tamburini et al., 2013). It is believed that biotopes under elevated pressure represent the largest habitat for microbial life on Earth, and pressure generally enhances microbial activity rates in deep environments (Picard and Daniel 2013). As a pioneer in piezophile studies, Bartlett and his collaborators have done a lot of work on how HHP impacts the biological processes in psychrophilic piezophilic bacteria, by investigating the changes of DNA replication, gene expression and regulation, respiratory system, flagellar systems, and genetic mutations under HHP (Tamegai et al., 2012; El-Hajj et al., 2009; Marietou et al., 2015; Eloe et al., 2008; Lauro et al., 2008). These works indicated the importance of unsaturated fatty acids proportion and increasing swimming velocity under HHP in a well-studied psychrophilic piezophilic bacteria strain, *Photobacterium profundum* SS9. Although their

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work in SS9 strain showed that the respiratory component was not affected by altered pressure, they came up an assumption that SS9 strain may use fermentation rather than respiration under high pressure (Tamegai et al., 2012). In addition, Fang et al. reported changes in the energy yields of redox reactions in the deep sea under low temperature and HHP conditions and compared these conditions to those of surface environments at 25 °C and 0.1 MPa (Fang et al., 2010). In recent studies, HHP was reported to impact the shifts of end products of fermentation and external electron acceptors in respiration in both the microbiological community and in pure cultured strains (Yang et al., 2020; Yin et al., 2017; Li et al., 2018). Considering the common effects of HHP on deep-sea microbes, Xiao et al. called for the scientific community to give more specific attention to HHP and its roles in shaping microbial physiology, community structure, and evolution (Xiao et al., 2021). Thus far, most studies of HHP effects on deep-sea microorganisms were focused on psychrophilic piezophilic bacteria, which left a huge knowledge gap for the microorganisms living in deep but hot environments.

1.2. High temperature environments with high biomass levels in the deep sea and subseafloor

Hydrothermal alteration processes driven by the internal heat of the earth are some of the most important and widespread geological processes in the oceanic crust, and the maximum circulating temperature of hydrothermal fluid is between ~500 and 700 °C (Wilcock and D. 1998). Hydrothermal circulation through the ocean crust plays a major role in controlling the chemistry of seawater, the operation of subduction zones, the growth of continents and the Earth's heat budget (Roberts and Bally 2012).

The hydrothermal circulation at plate boundaries forms the hydrothermal vents, the 'black' and 'white' smokers, with high fluid temperatures of ~400 °C and ~200–330 °C, respectively (Fig. 1) (Macdonald 2007). Hydrothermal vents are typical high-temperature environments in the deep sea and are known to be common at continental margins and oceanic spreading centers worldwide (Campbell 2006). Collectively, these hydrothermal systems are responsible for ~20% of the total heat loss of the Earth and have a major impact on ocean and solid earth chemistry (Staudigel 2003). Vent fluids are formed from the cold seawater (2–4 °C) infiltrating into the ocean crust through cracks. The fluid is heated during its journey through the crust, and the temperature gradually increases to a point as high as 400 °C and finally erupts from the chimney (Dissanayake et al., 2014). Around the chimney, fluids that are hot (up to 405 °C), acidic (pH 2–3), and rich in reducing substances (such as Fe^{2+}, H_2S, H_2, etc.) quickly cool down in the surroundings seawater, which is cold (2–4 °C), alkaline (~pH 8) and rich in oxidizing substances (such as Fe^{3+}, O_2, etc.). This process creates drastic gradients of temperature (2–400 °C), pH (2–8), redox, salinity and other physical and chemical parameters near the vents (Martin et al., 2008). Redox gradients provide the main energy sources for microorganisms living in hydrothermal vents. The variable temperatures arising during the hydrothermal vent processes have shaped the microbiological community and challenged the survival and growth of life. In addition to the high temperatures, hydrothermal vents are characterized by high hydrostatic pressure, with water depths ranging from ~1000–~5000 m (Connelly et al., 2012) and with an average depth of ~2000 m; this exerts pressures ranging from ~10 to 50 MPa with an average pressure of ~20 MPa. In addition, pressures also increase with the depth of sediments, ~15 MPa per kilometer (Cario et al., 2019).Thus far, the highest temperature on Earth's surface reached ~500 °C in the deepest (~5000 m) known hydrothermal vents, the Piccard hydrothermal field in the Mid-Cayman Rise (Mcdermott et al., 2018). Although hydrothermal vents are among the most extreme environments on the Earth and exhibit dramatic environmental fluctuations, they have shown extremely high biodiversity and support ecosystems with enormous biomass and productivity compared with those observed elsewhere in the deep oceans (Brazelton 2017; Zierenberg et al., 2000). In the past four decades, thermophilic and hyperthermophilic microorganisms, such as bacteria, archaea and viruses (that can infect thermophiles and hyperthermophiles) (Prangishvili and Garrett 2004; Geslin et al., 2003; Gorlas et al., 2012), have been widely found, isolated, and investigated (Grogan 2013), which greatly broadens our understanding of lifestyles and metabolic diversity at high temperatures. However, most studies on hydrothermal microorganisms are carried out under atmospheric pressure, which leaves blind spots regarding the life processes in deep-sea hydrothermal vents (Xiao et al., 2021).

In addition to the hydrothermal vents, deep sediments beneath the subseafloor are also typical high-temperature environments in the deep sea, but they are much less well known (Fig. 1). Sediments normally accumulate from the 5–10 billion tons of particulate matter that is constantly sinking within the oceans. These sediment layers are very extensive and can be up to 10 km thick, with an average depth of 500 m (Sass and Parkes 2011). Although the surface sediments are cold (~2 °C), temperatures increase gradually with depth. Sediments warmer than 40 °C account for roughly half the marine sediment volume (Heuer et al., 2020). A global quantified three-dimensional model revealed that

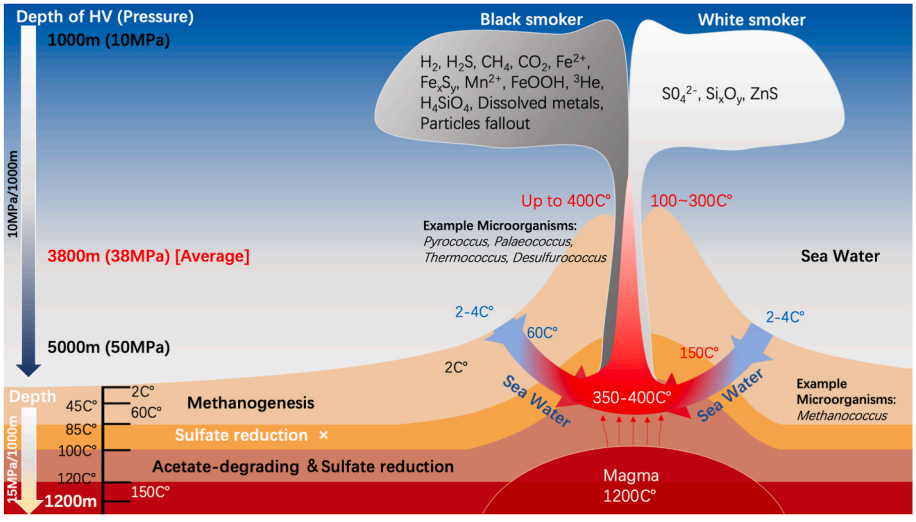

Fig. 1. Schematic diagram of high temperature environments under deep-sea high hydrostatic pressure. Temperatures and microbial activities with different sediment depth were referred from data by Heuer et al. (Heuer et al., 2020). HV: hydrothermal vent.

~35% of sediments are warmer than 60 °C, and ~25% of marine sediments are warmer than ~80 °C (Larowe et al., 2017). Considering the 3800 m average depth of oceans (with pressures of 38 MPa) and the lithostatic pressure found with increasing depths of sediments and crust (Oger and Jebbar 2010), microbes in the subseafloor often encounter and must survive conditions of high hydrostatic pressure, high temperature, and, sometime, extreme starvations (Fouquet 2014; Peoples et al., 2020). However, the subseafloor biosphere is still suggested to contain two-thirds of Earth's total prokaryotic biomass (Whitman et al., 1998). It is known that subseafloor microbes play a significant role in chemical reactions that were previously thought to have been abiotic, including iron and sulfur cycling as well as ethane and propane generation (Hinrichs et al., 2006). However, the limits of subsurface life in terms of any environmental properties are not yet known due to the lack of testable cultures.

1.3. What is the upper temperature limit for life under HHP?

As the record for the deepest sediments has been raised several times, the record for sedimentary microorganisms living at high temperatures has also been updated (Roussel et al., 2008; Heuer et al., 2020) (Fig. 2). In 2008, Roussel et al. provided evidence of prokaryotic cells living 1626 m below seafloor (mbsf) sediments at temperatures of 60–100 °C, and suggested that representative hyperthermophile, Thermococcales (i.e., *Thermococcus* and *Pyrococcus*), is the only group active in the deep biosphere at that depth (Roussel et al., 2008). In a recent study, Heuer et al. provided evidence for growing microbes living up to a depth of 1.2 km with hot sediments up to 120 °C in the Nankai Trough subduction zone. The microbiological metabolic activities are distinguished by different temperature zones. Above 45 °C to 80–85 °C, the biological production and oxidation of methane are detected, while at 100 °C–120 °C, the activity of acetate-degrading hyperthermophiles is detected. These results suggested that temperature is one of the key factors shaping the metabolic processes occurring in deep sediments, and further shows that life in the deep subseafloor is not constrained by an upper temperature limit below 120 °C (Heuer et al., 2020).

For pure cultured microbes, the record for the highest growth temperature has been raised several times in the past five decades. Thermophiles were first discovered in the hot springs of Yellowstone National Park in the United States, and their highest growth temperatures could be as high as 89 °C, which was recorded as for chlorophylless *Schizomycetes* in 1903 (Setchell 1903). Thermophilic bacteria with a maximum growth temperature of 93 °C were discovered in the 1960s and 1970s (Brock 1978). With the discovery of hydrothermal vents in the 1980s, hyperthermophiles whose maximum growth temperatures exceeded 100 °C were isolated there (Baross et al., 1982). This is the first time it was realized that the upper temperature of life can reach 100 °C. Thus far, microbes with the ability to grow at and above approximately 100 °C are all archaea (Grogan 2013). In 1997, a *Pyrolobus fumarii* strain with a maximum growth temperature of 113 °C was isolated (Stetter 2006). In 2008, Takai et al. extended the maximum growth temperature of the *Methanopyrus kandleri* 116 strain to 122 °C by increasing the pressure to 20 MPa (Patra et al., 2018). This record has lasted until now. Although the highest growth temperature reported for individual life is 122 °C, environmental and theoretical studies suggest that the upper limit of life might be ~150 °C, due primarily to the instability of macromolecules above this temperature (Merino et al., 2019). The gaps among the highest known temperature of life (122 °C), the theoretical upper limits of macromolecules (~150 °C) and the high temperatures of environments (>400 °C) has triggered the following question: where should be the real upper temperature boundary of life be placed, especially when one considers the effects of HHP?

2. Physiological correlations between high temperature and HHP

Both thermophilic bacteria and hyperthermophilic archaea can be piezophiles, but above 85 °C all the reported thermophilic piezophiles are archaea. All of them have a much higher maximum growth pressure than the *in situ* pressure caused by water depth, and most of them have an optimal growth pressure higher than that found *in situ* (Table 1). In previous studies, it was found that growth at a higher temperature usually requires a higher pressure. As a special conditional piezophile example, *Thermococcus eurythermalis* A501 acts as a piezotolerant strain with an optimal growth pressure of 0.1–30 MPa at 85 °C, while at 95 °C it is an uncontroversial piezophile with an optimal growth pressure of 10 MPa (Zhao et al., 2015). On the other hand, the optimal or/and maximum growth temperature of some thermophilic piezophiles can be extended by increasing the HHP (Table 1). As an example, studies of *Methanocaldococcus jannaschii* JAL-1 showed that the optimal growth temperature increased from 72 °C to 86 °C at 7.5 MPa, and its growth rate increased by three times at atmospheric pressure and 88 °C (Jones et al., 1983). As mentioned above, the highest known growth temperature of microorganisms is 122 °C, which was recorded for *Methanopyrus kandleri* 116 (Kurr et al., 1991) by culturing at 20 MPa (Takai et al., 2008). Interestingly, at 0.1 MPa, the highest growth temperature of strain 116 was only 110 °C. As the pressure increased to 0.4 MPa, the highest growth temperature increased to 116 °C (it did not grow further when the temperature increased to 118 °C). When the pressure increased to 20 MPa, the highest growth temperature increased to 122 °C. All these phenomena suggested a physiological correlation between high temperature and HHP in hyperthermophiles. When hyperthermophiles face some kinds of damage under a lethal high temperature, HHP may be a favorable environmental factor allowing

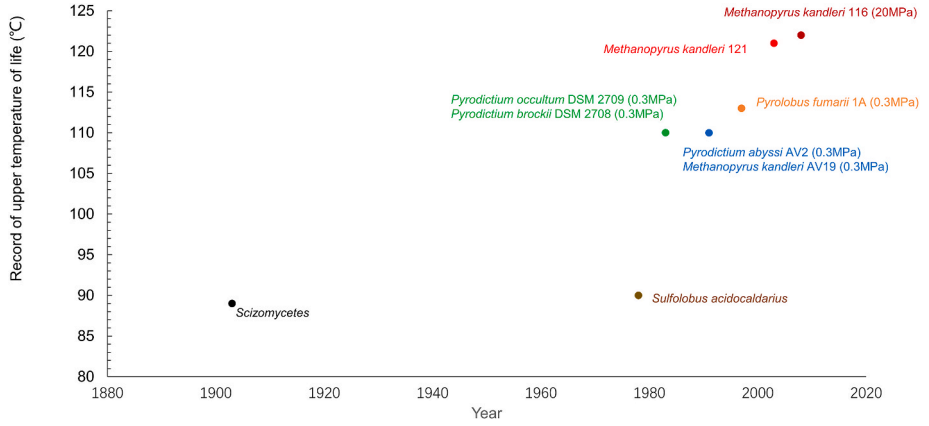

Fig. 2. Record of upper temperature of life. Numbers in brackets represent the hydrostatic pressures to support the growth at the corresponding temperatures (some pressure data can refer to the main text).

Table 1
Reported (hyper)thermophilic piezophiles including both bacteria and archaea. Abbreviations: Topt: optimal growth temperature; Tmax: maximum growth temperature; Popt: optimal growth pressure; DSHV: deep sea hydrothermal vents; DSHS: deep sea hydrothermal sediments; SGHSF: sandy geothermally heated sea floor; ND: no data.

Type	Strain name	Habitats	*in situ* depth (m)	Topt (°C)	Tmax (°C)	Popt (MPa)	P range (MPa)	Energy metabolism	Reference
Bacteria	*Anoxybacter fermentans* DY22613	DSHV	2891	60–62	72	20	0.1–60	Fe^{3+} reduction	Zeng et al. (2015)
	Piezobacter thermophilus 108	DSHV	3626	50	55	35	0.1–65	H_2/S oxidation	Takai et al. (2009)
	Thioprofundum lithotrophica 106	DSHV	3626	50	55	15	0.1–50	S oxidation	Takai et al. (2009)
	Thermosipho japonicus IHB1	DSHV	972	65	70	20	0.1–60	S reduction	Takai and Horikoshi (2000)
	Marinitoga piezophila KA3	DSHV	2630	60	70	40	0.3–50	S reduction	Alain et al. (2002)
	Pseudothermotoga elfii DSM9442	DOW	1600–1900	66	72	20	0.1–50	Fermentation	(Roumagnac et al., 2020; Ravot et al., 1995)
	Clostridium paradoxum JW-YL-7	WGAP	–	56 (0.1 MPa) 60 (22 MPa)	63 (0.1 MPa) 70 (22 MPa)	22	0.1–30	Methanogenesis	(Li et al., 1993; Scoma et al., 2019)
Archaea	*Methanocaldococcus jannaschii* JAL-1	DSHV	2600	72 (0.01 MPa)86 (7.5 MPa)	95	ND	0.1–75[a]	Methanogenesis	(Jones et al., 1983; Boonyaratanakornkit 2006)
	Methanococcus thermolithotrophicus DSM 2095	SGHSF	0.5	65	70	50	0.1–100	Methanogenesis	Huber et al. (1982)
	Methanopyrus kandleri 116	DSHV	2000	105	110 (0.1 MPa)116 (0.4 MPa)122 (20 MPa)	20	0.1–50	Methanogenesis	(Kurr et al., 1991; Takai et al., 2008)
	Methanopyrus kandleri 121	DSHV	2270	105	121	ND	ND	Fe^{3+} reduction	Kashefi and Lovley (2003)
	Palaeococcus ferrophilus DMJ	DSHV	1338	83	88	30	0.1–60	S reduction	Takai et al. (2000)
	Palaeococcus pacificus DY20341	DSHS	2737	80	90	30	0.1–80	S reduction	Zeng et al. (2012)
	Pyrococcus abyssi GE5	DSHV	2000	96	102 (0.2 MPa)105 (20/40 MPa)	20	0.1–50	S reduction	Erauso et al. (1993)
	Pyrococcus yayanosii CH1	DSHV	4100	98	105 (20 MPa) 108 (52 MPa)	52	20–120	S reduction	Birrien et al. (2011)
	Thermococcus aggregans TY	DSHV	2000	88	94	20	0.1–30	S reduction	Canganella et al. (1998)
	Thermococcus guaymasensis TYS	DSHV	2000	85	90	20–35	0.1–50	S reduction	Canganella et al. (1998)
	Thermococcus peptonophilus SM-2	DSHV	2885	90	103	45	0.1–60	S reduction	González et al. (1995)
	Thermococcus eurythermalis A501	DSHV	2007	85	100 (0.1 MPa)102 (40 MPa)	0.1–30 (85 °C)10 (95 °C)	0.1–70	S reduction	Zhao et al. (2015)
	Thermococcus barophilus MP	DSHV	3550	85	95 (0.3 MPa) 100 (40 MPa)	40	0.1–80	S reduction	Marteinsson et al. (1999)
	Thermococcus paralvinellae ES1	DSHV	2200	88	93 (1 MPa) 95 (22 MPa)	40	ND	S reduction	Hensley et al. (2014)
	Thermococcus piezophilus CDGS	DSHV	4964	75	90 (50 MPa)	50	0.1–125	S reduction	Dalmasso et al. (2016)
	Thermococcus barophilus Ch5	DSHV	3020	88	ND	40	ND	S reduction	(Oger et al., 2016; Zhang et al., 2021)
	Thermococcus camini Iri35c	DSHV	2300	75–80	90	10–30	.01–50	S reduction	Courtine et al. (2021)
	Pyrococcus strain ES4	DSHV	2200	97	95 (3 MPa) 105 (22 MPa)	ND	ND	S reduction	Holden and Baross (1995)
	Pyrococcus sp. GB-D	DSHV	2010	90	95 (0.1 MPa) 104 (10/20 MPa)	ND	ND	S reduction	Jannasch et al. (1992)
	Desulfurococcus sp. SY	DSHV	2510	90	94 (0.1 MPa) 96 (10/20 MPa)	ND	ND	S reduction	Jannasch et al. (1988)
	Archeoglobus fulgidus VC-16	heated sea floor	ND	85	95	0.1–60	0.1–30	Sulfate reduction	(Oliver et al., 2020; Stetter 1988)

Abbreviations. Topt: optimal growth temperature; Tmax: maximum growth temperature; Popt: optimal growth pressure; DSHV: deep sea hydrothermal vents; DSHS: deep sea hydrothermal sediments; SGHSF: sandy geothermally heated sea floor; DOW: deep oil-producing well; ND: no data.

[a] For *M. jannaschii* strain, 75 MPa corresponds to the highest pressure tested, with a higher growth rate but the optimum pressure is not known (Miller et al., 1988).

them to maintain and survive. The current 122 °C record at 20 MPa provides a potential opportunity to investigate the upper temperature limits of life by considering the effects of HHP.

The optimal growth temperature of microorganisms has been proved to be closely related to the nucleic acid sequence of the genome (Sauer et al., 2019). Using statistical and machine learning methods, Li et al. developed software that uses protein sequences annotated from the complete genome to predict the optimal growth temperature of microorganisms (Li et al., 2019). This software can accurately predict the optimum growth temperature from the microbial dipeptide sequence, and the catalytic temperature of an enzyme can be predicted for the subsequent amino acid sequence of the individual enzyme. We used this method to predict the optimal growth temperature of some piezophilic hyperthermophiles mentioned above (Table 2). The software gave overall accurate predictions, but when the experimental optimum growth temperature was over 90 °C (especially 95 °C), a 4–5 °C deviation was observed. On the one hand, the deviation may be caused by a larger base of the optimum growth temperatures; on the other hand, thermophiles with optimum growth temperatures over 95 °C may have a special thermal stability mechanism. In addition to the stability of the protein structures of large molecules, there are other mechanisms favoring adaptation to the high temperature environments. By using the training set data model and the microbial optimal growth temperature prediction model of the software, one can, in theory, adjust the software to predict the relationship of microbial maximum growth temperature by replacing the training data set; but the optimum growth temperature and the highest temperature of the microorganism do not exhibit a linear relationship between, which means that the highest temperatures of microorganisms are not completely determined by the genome. Therefore, the software predictions of the temperature adjustment needed to obtain the highest growth temperature may not be completely accurate.

3. HHP helps to maintain biological integrity at high temperature

In this section, we review the knowledge and potential puzzles arising from studies on water chemistry, the stability of cell membranes and macromolecules, and the synthesis and accumulation of molecular chaperones and compatible solutes under high temperatures and HHP. In these situations, some negative impacts on cells and cellular components caused by high temperature can be alleviated by HHP to a certain level. It is generally true that HHP helps cells to maintain biological integrity at high temperatures (Fig. 3).

3.1. Water

H_2O is a special inorganic molecule. Liquid water is the main components of all cells (>70% of wet weight), and it plays an irreplaceable role in maintaining functional cells and driving all biological processes (Ling 2006). When heated above 100 °C, it usually requires a pressure higher than atmospheric pressure to maintain the liquid condition of both intercellular and extracellular water, or it can no longer participate in biological processes and biochemical reactions as a medium and solvent. High temperature also influences aspects of the water chemistry, e.g., by reducing the solubilities of gases and/or byproducts (e.g., H_2, H_2S, CO_2, O_2, etc) (Golubev et al., 2014). HHP has the opposite effect on solubility, relative to increasing temperature, and it helps cells maintaining feasible rates for gas uptake and removal of toxic byproducts. Furthermore, high temperature physically disturbs all kinds of bonds, including hydrogen bonds; however, hydrogen bonding may increase under HHP, as revealed by molecular dynamics investigations (Root and Berne 1997). This contrasting effect of HHP on hydrogen bonds helps to maintain water-water and water-macromolecular interactions at high temperatures (Fig. 3A).

Thus far, most of the physical effects of high temperature and/or HHP were determined from experiments and/or computational simulations on pure solvents or mixtures of solvents (e.g., water and glycerol). With the development of physical detection technologies, water and hydrogen bonds within cellular components and living cells have attracted great interest among both physicists and biologists in recent studies. Shrestha et al. used the quasielastic neutron scattering (QENS) technique to investigate the effects of HHP (100 MPa) on the conformational flexibility and relaxation dynamics of an oligomeric protein, inorganic pyrophosphatase (IPPase), taken from a hyperthermophile found near deep-sea hydrothermal vents exhibiting temperature spanning a wide range from −53 °C to 80 °C. The authors observed faster

Table 2
Comparison between the prediction of optimal growth temperature of piezophilic hyperthermophiles and the experimental results. The machine learning based temperature prediction was followed the method developed by Li et al., (2019). The model was trained by the default OGT dataset (21, 498 microorganisms) associated with the software (https://github.com/EngqvistLab/Tome), with following parameters: root-mean-square error (RMSE) 2.159, R^2 score 0.955, Pearson r (0.978, 0.0) and Spearman correlation 0.933 (p-value 0.0). Amino acids sequences of CDSs in complete genome of each strain were used to predict the optimal growth temperature.

Strain	No. CDS	Topt-predicted (°C)	Topt-experimental (°C)	Difference (°C)	Tmax-experimental (°C)	Reference
Marinitoga piezophila KA3	2, 077	62.5	65	2.5	70	Alain et al. (2002) NCBI: GCA_000816105.1 ASM81610v1
Palaeococcus ferrophilus DMJ	2, 350	80.0	83	3.0	88	Takai et al. (2000) NCBI: GCA_000966265.1 ASM96626v1
Thermococcus barophilus MP	2, 228	83.6	85	1.4	100	Marteinsson et al. (1999) NCBI: GCA_000151105.2
Thermococcus peptonophilus OG-1	2, 059	83.3	85	1.7	100	(González et al., 1995; Kato et al., 2010) NCBI: GCA_001315905.1
Thermococcus guaymasensis TYS	2, 107	86.9	88	1.1	90	Canganella et al. (1998) NCBI: GCA_000816105.1 ASM81610v1
Pyrococcus abyssi GE5	1, 915	90.5	96	5.5	102	Erauso et al. (1993) NCBI: GCA_000195935.2 ASM19593v2
Pyrococcus yayanosii CH1	1, 882	94.0	98	4.0	108	Birrien et al. (2011) NCBI: GCA_000215995.1 ASM21599v1
Pyrococcus yayanosii A1	1, 886	94.0	98	4.0	108	(Unpublished data)
Methanopyrus kandleri AV-1	1, 814	97.1	98	0.9	110	Kurr et al. (1991) NCBI: GCA_013329715.1

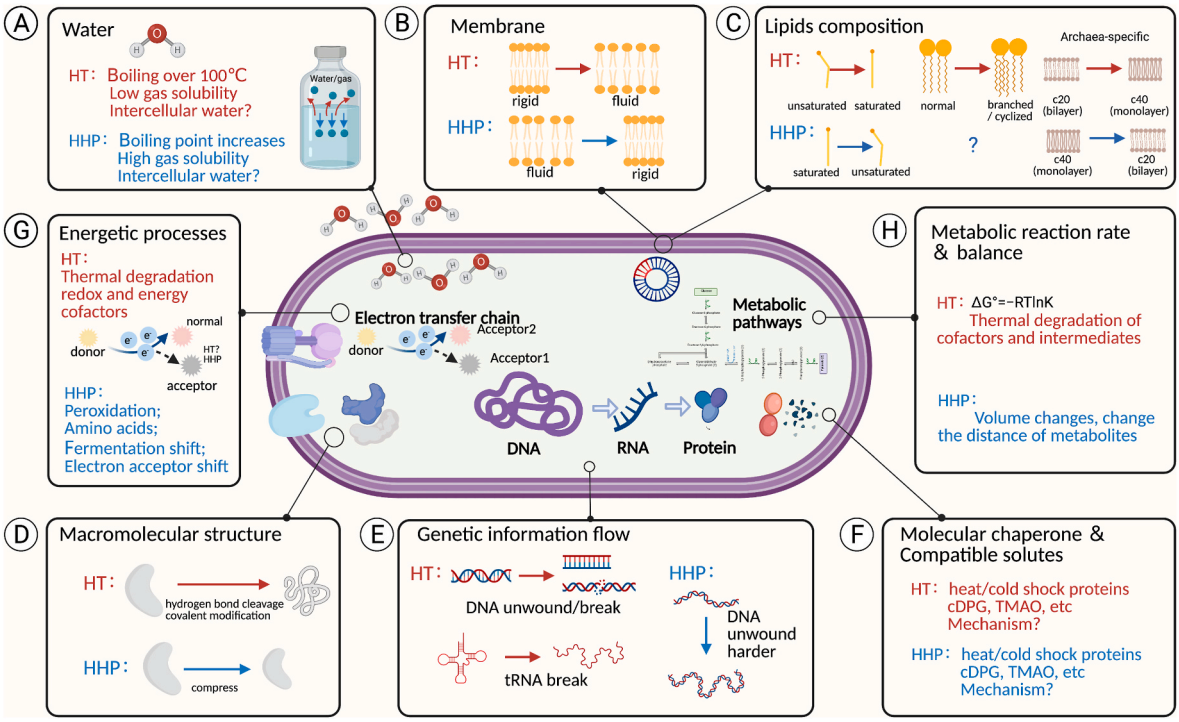

Fig. 3. Schematic diagram of the effects of high temperature and high hydrostatic pressure on cells and biological processes in (hyper)thermophilic piezophiles. HT: high temperature; HHP: high hydrostatic pressure.

relaxation dynamics in this hyperthermophilic protein than in a mesophilic model protein, which provides evidence that the protein energy landscape is distorted by high pressure and is significantly different for hyperthermophilic and mesophilic proteins (Shrestha et al., 2015). Tros et al. used ultrafast vibrational spectroscopy and dielectric relaxation spectroscopy to observe the random orientational motions of water molecules inside the living cells of three prototypical mesophilic organisms. They found that most of the intracellular water exhibited the same random orientational motion as neat water, whereas a smaller fraction (~20–45%) exhibited slower orientational dynamics. This intercellular slow water is proposed to bound primarily to proteins and, to a lesser extent, to other biomolecules and ions (Tros et al., 2017). In addition, the high flexibility of proteome associated with reduced hydration water was observed in hyperthermophilic piezophilic archaea by using quasi-elastic neutron scattering, which was proposed to be a potential key to the molecular adaptation of the cells to high hydrostatic pressure (Martinez et al., 2016). However, the detailed physical effects of temperature and/or pressure on intercellular water in both mesophilic and (hyper)thermophilic conditions remain a mystery.

3.2. Cell membrane

The cell membrane is essential for separating the intracellular environment from the outside. The existence of the membrane enables the cell to maintain a relatively stable internal environment to support biological functions in the face of changing or extreme external environments. The mobility of the cell membrane increases at high temperatures (Fig. 3B). With the application of lethal heat stress, the high mobility of the cell membrane easily leads to the appearance of pores and structural damage, which cause solute overflow and cell lysis. In addition, lethal heat stress also has a great impact on binding of membrane proteins and the permeability of cell membrane. At lethal high temperatures, membrane proteins aggregate, membrane protein activity decreases, solute flux decreases, and the permeability of cations increases (Lande and B. 1995).

Hyperthermophiles themselves have special membrane properties allowing them to adapt to high growth temperatures. For example, thermophilic bacteria enhance the thermal stability of membranes by increasing the proportion of saturated fatty acids in phospholipid molecules, increasing the length of phospholipid alkyl chains and increasing the proportion of isomerized branched chains (Imanaka 2011). Hyperthermophilic archaea use a monolayer membrane structure comprising glycerol dibiphytanyl glycerol tetraethers (GDGTs), which are more rigid and impermeable than classical bacterial/eukaryal bilayer membranes made of diacylglycerols; GDGTs impact higher mechanical strength to resist the high-temperature environments (Chong 2010). In addition, the increase in cyclopentane structures and the glycosylation modification of the glycerol skeleton are also ways for hyperthermophilic archaea to maintain the stability of membrane (Ulrih et al., 2009). Most of these adaptation mechanisms enhance stability through changing membrane lipids and their composition.

Generally, HHP helps maintain membrane integrity, fluidity, and permeability, like the low temperature treatment, leading to contrasting results at high temperatures (Fig. 3B). HHP and low temperature can both make the cell membrane orderly and compress the packing of fatty acids (Daniel et al., 2006). At 100 MPa and 2 °C, the fluidity of the membrane is similar to that seen at −18 °C under a pressure of 0.1 MPa (Simonato et al., 2006). Each 10 MPa increase in pressure is equivalent to a 13–21 °C decrease in temperature, but the exact equivalence is determined by the composition of the lipid system (Somero 1992). High temperature increases the entropy of the membrane and increase its disorder, while high pressure will reduce the entropy. The increase in pressure reduces the fluidity of the membrane, so HHP can maintain the fluidity of the membrane within a relatively stable range. For membrane proteins, on the one hand (as mentioned above), the increase in hydrostatic pressure is conducive to the maintenance of the protein's structure to a certain extent, so HHP can maintain the protein's higher structure resist the damage caused by high temperatures. On the other hand, due to the increased accumulation of lipid chains, HHP can cause changes in protein-membrane interactions (Scarlata 2005). The influence of HHP on the membrane structure can maintain the stability of the membrane and the normal function of the membrane when

thermophiles are subjected to lethal thermal stress, and this is one of the ways that HHP can increase the maximum temperature and maintain the integrity of the cell structure.

Almost all archaea produce both diethers and tetraethers (Tourte et al., 2020; Oger and Cario 2013). Many works to date have demonstrated a strong correlation between the diether/tetraether ratio in lipid composition and adaptation to various extreme conditions in addition to high temperature, such as extreme acidity, alkalinity, salinity, and HHP (Boyd et al., 2013; Kates 1993; Cario et al., 2015). Cario et al. measured the ratio of diether (C20, Archaeol) versus tetraether (C40, GDGT-0) under different temperatures and pressures (Fig. 3C). Their results clearly showed the similar trends with increasing pressure and decreasing temperature, both of which led to an increase in the proportion of diethers. Conversely, a higher proportion of GDGT-0 was observed under low-pressure and high-temperature conditions. Notably, fluctuations in pressure and temperature also impacted the level of unsaturation of apolar lipids with an irregular polyisoprenoid carbon skeleton (unsaturated lycopane derivatives) (Cario et al., 2015) (Fig. 3C).

3.3. Macromolecules

Many biomolecules, especially the macromolecules, face different threats under heat stress. The effect of high temperature on biological stability is the most studied of these threats. Hydrogen bond is a kind of weak interaction and hydrogen bonds in proteins help to stabilize protein structure (Steiner 2002). For protein molecules, irreversible denaturation occurs when the hydrogen bonds inside the protein are broken under the influence of deadly thermal stress (Scharnagl et al., 2005). At the same time, amino acid residues in protein molecules are prone to undergo covalent modifications at high temperature, leading to the inactivation and degradation of protein molecules such as in the deamidation of glutamine residues and asparagine residues and the oxidation of cysteine residues (Jaenicke and Sterner 2006) (Fig. 3D). The nucleic acid molecules DNA and RNA are also threatened by high temperatures. The double helix of the DNA molecule will open when the temperature exceeds the DNA melting temperature, and the structure of the tRNA molecule is easily destroyed at high temperature (Jaenicke and Sterner 2006), and it cannot participate in the functional translation process (Fig. 3E).

Hyperthermophiles exhibit special adaptation mechanisms for adapting to "optimal growth" temperature conditions, such as enhancing noncovalent forces (Littlechild et al., 2013), improving the stability of α-helices (Sterner and Liebl 2001), and reducing hydrophobic effects (Holden and Daniel 2004). However, when hyperthermophiles face nearly lethal thermal stress, these high-temperature adaptation mechanisms cannot effectively maintain the functional activities of cells. In this scenario, HHP can help maintaining the stability of these biomolecules to some extent. For example, Derek et al. found that high pressure can help maintaining the stability of hydrogenase of *M. jannaschii*; based on their results, this effect was proposed to play a role by establishing hydrophobic interactions. The authors also analyzed how HHP helped to maintain the internal packaging of amino acids to preserve stability (Hei and Clark 1994). HHP promotes protein compression and mitigates the damage of the three-dimensional structure caused by the loss of protein hydrogen bonds induced by high temperature (Welch et al., 1993). Additionally, HHP helps stabilize the structure of DNA and RNA and helps RNA function normally at high temperature (Daniel et al., 2006). Since HHP can stabilize DNA hydrogen bonds, the melting temperature of DNA increases with the increase of pressure (Chong et al. 2003, 2005). The stacked interaction with a negative volume change under high pressure can also help stabilize the double helix structure (Daniel et al., 2006) (Fig. 3E).

3.4. Molecular chaperones and compatible solutes

Molecular chaperones are proteins that bind to macromolecules to help maintain structure and function, including the most common groups of heat shock proteins and cold shock proteins (Melnikov and Rotanova 2010). They assist in *de novo* protein folding, stabilize proteins under stresses and maintain polypeptide chains in a loosely folded state competent for translocation across membranes (Hartl and Martin 1995). For example, Hsp 70 and Hsc 70 helped to elevate tolerance to hyperthermia (Feder and Hofmann 1999). Studies of *Escherichia coli* under HHP and high temperature showed that HHP induced the production of 11 heat shock proteins and 4 cold shock proteins, which is the largest known collection of heat/cold shock proteins induced at the same time. These heat and cold shock proteins helped to maintain the amino acid interactions that allow proteins to fold correctly and resist a high-temperature environment (Dong et al., 2008) (Fig. 3F).

Compatible solutes are small molecule secondary metabolites that increase the water activity in cells to balance the osmotic pressure inside and outside cells, and most of them are osmolytes required for osmotic adjustments (Bohnert and Shen 1998). They do not interfere with protein structure and function, and they alleviate the inhibitory effects of high ion concentrations on enzyme activity. Hyperthermophiles synthesize and accumulate some special compatible solutes *de novo*, which distinguishes from the mesophiles. For example, di-myoinositol-1, 1′-phosphate (DIP) and mannosylglycerate (MG), negatively charged derivates from mesophilic osmolytes, are widespread in hyperthermophilic archaea (e.g., *Thermococcus* and *Pyrococcus*), restricted to certain thermophilic bacteria taxa (e.g., *Thermotoga* and *Aquifex*) and are commonly missing among mesophiles (Lentzen and Schwarz 2006; Santos et al., 2007; Gerday 2008). These hyperthermophile-specific compatible solutes are often known to synthesize and accumulate solutes under both optimal and higher temperature conditions, and are supposed to stabilize the structures of macromolecules against thermal denaturation (Santos and Costa 2010).

Recent studies have revealed that biosynthesis and accumulation of compatible solutes is a universal adaptation mechanism for responding to various environmental stresses, including high temperature and HHP (Zhao et al., 2020). For example, in isolates, cyclic 2,3-diphosphoglycerate (cDPG), a cyclic trianionic pyrophosphate that was first detected in the thermophilic methanogen *Methanothermobacter thermoautotrophicus*, accumulates at high temperature and has been shown to stabilize archaeal glyceradehyde-3-phosphate at high temperature (Lentzen and Schwarz 2006). Transcriptomic and proteomic data indicated the possibility that HHP induced cDPG biosynthesis in hyperthermophilic piezophiles (Michoud and Jebbar 2016; Zhao et al., 2020). Cario et al. also reported the accumulation of MG in response to the thermal and salinity stresses, and drastically increased under the sub-optimal pressure in hyperthermophilic piezophile *T. barophilus* MP (Cario et al., 2016). Salvador-Castell et al. recently provided evidence for a protecting effect of the presence of the osmolyte MG on proteome under low pressure stress in *T. barophilus* MP by investigating water motions via neutron scattering techniques. It was found that the mutant strain, with the absence of MG, is less crowded and presents similarly as the lysed cells, where the crowding effect is highly diminished, thus the strain without MG has a more pressure-sensitive dynamics (Salvador-Castell et al., 2019). Other examples in the environment are TMAO and glycine, which are used as osmolytes to help microorganisms adapt to high-temperature and HHP environments; they help to maintain the structure of proteins, antagonize the hairpin structure of nucleic acid molecules, and maintain the stability of the membrane structure (Patra et al., 2018; Jaworek et al., 2018; Manisegaran et al., 2019) (Fig. 3F). Petrov et al. showed the results that TMAO helps to counteract the effect of HHP up to 40 MPa on the MscS/MscK open state by "shielding" the cytoplasmic domain of the channels (Petrov et al., 2012). In total, HHP-induced the biosynthesis and/or accumulation of some osmolytes in cells not only helps resist HHP conditions, but also helps organisms to

deal with the cell damage caused by lethal heat stress. The accumulation of multiple compatible solutes and their *de novo* biosynthesis pathways have been identified and shown to be associated with various stresses, but little is known about their *in vivo* physical, physiological, and metabolic roles, which leaves a huge knowledge gap in our understanding of how compatible solutes work in cells. It deserved to extend studies on more hyperthermophilic microorganisms from the deep biosphere.

4. Both high temperature and HHP challenge the metabolic feasibility

Hyperthermophilic microorganisms are all chemotrophic microorganisms, including chemoautotrophs and chemoheterotrophs. The chemoautotrophic microorganisms are mainly anaerobic, and a few are micro-oxygenated. They carry out energy metabolism through the oxidation of H_2 and S, as well as the recovery of S, SO_4^{2-}, CO_2 and NO^{3-} (Schönheit and SchönheitJ 1995). The metabolic pathways of chemoheterotrophic hyperthermophiles mainly include the metabolism of peptides and sugars as substrates. Their energy metabolism is very diverse and involves the use of different kinds of electron acceptors, such as Fe^{3+}, CO_2, NO^{3-}, sulfur compounds in different oxidation states, and even protons (Schönheit and SchönheitJ 1995). Some of them contain more than one electron acceptor in the electron transfer chain. With the presence of external electron acceptors, the substrates will be oxidized to CO_2 and/or converted to other organic products with low molecular weights (e.g., acetate, propionate, alcohols) by fermentation (Schönheit and SchönheitJ 1995). Hyperthermophiles have special characteristics in their metabolic pathways to address challenges of thermal stresses, but they still suffer from chemical reaction imbalances, accumulation of toxic metabolites and losses in coupling efficiency caused by temperature disturbances. Similarly, HHP also has global impacts on metabolism, as mentioned from the very beginning. Therefore, the dual-stress conditions of high temperature and HHP will cause additive influences on metabolism. In this section, we summarized the reported challenges and potential inferences on metabolic influences at high temperature and HHP (Fig. 3), although the final additive effects and the underlying metabolic mechanisms are still unclear due to the lack of systematic studies.

4.1. Spontaneous thermal degradation of key metabolites

At high temperature, some small molecule metabolites are unstable, resulting in the destruction of the entire chemical reaction balance (Daniel and Cowan 2000). The most influential problem is the thermal degradation of electron and energy carriers. The redox cofactors NAD(P)$^+$ and the energy compounds ATP/ADP are all hydrolyzed when the temperature reaches 100 °C (Jaenicke and Sterner 2006). NAD(P)$^+$ is an important cofactor for enzymatic oxidation reactions in all living organisms. It has been confirmed to be susceptible to thermal degradation in hyperthermophiles, and its half-life is less than 10 min at 100 °C (Jaenicke and Sterner 2006), which is usually not appropriate for biocatalysis at high temperature (>95 °C) (Hofmann et al., 2010). Hyperthermophilic archaea harbor mechanisms that maintain *in vivo* NAD(P)$^+$ concentrations and possibly remove and/or reuse undesirable degradation products of NAD(P)$^+$. Thermal degradation of NAD(P)$^+$ results mostly in the generation of nicotinamide and ADP-ribose, and the latter is then converted to ribose 5-phosphate and AMP, which can be directed to central carbon metabolism (Hachisuka et al., 2017). The salvage pathway in hyperthermophiles can mitigate some negative influence of thermal degradation, but it still requires extra carbon and energy sources to produce NAD(P)$^+$ under thermal stresses.

HHP can affect the equilibria of the physicochemical reactions by influencing the volume changes of the reactions (Bartlett 2002). When a reaction is accompanied by a decrease in the volume of the reacting system, HHP can promote the reaction to a certain extent; when a reaction is accompanied by an increase in volume, it will be inhibited by increasing pressure (Abe 2007). Thermodynamically, high pressure can drive some exothermic reactions in which the reaction volume decreases or endothermic reactions in which the reaction volume increases. Thus, physical effects of HHP can theoretically compensate for some of the effects of thermal degradation.

4.2. Gibbs free energy changes under high temperature

Biochemical reactions are the foundation of metabolism in all living cells. Based on the Arrhenius formula, temperature is the most influential parameters driving biochemical reactions. High temperature has some advantages that make some chemical reactions feasible. For example, a common reaction in anaerobic environments, the conversion of formate and water to bicarbonate and hydrogen (with a change in Gibbs free energy of $\Delta G^\circ = +1.3$ kJ/mol), has not been considered sufficiently energetic to support the growth of microorganisms. However, hyperthermophilic archaea belonging to the *Thermococcus* genus can use this reaction, with the actual ΔG values ranging between −8 and −20 kJ/mol under the physiological conditions at the high temperature (80 °C) under which they are grown (Kim et al., 2010). On the other hand, because of the effects of high temperature on Gibbs free energy, increased temperatures can also interrupt the balance of biochemical reactions. For endothermic reactions, heat can inhibit the reaction operating under most conditions, whereas for exothermic reactions, the opposite is the case. Therefore, when cells face lethal heat stress, the accumulation of toxic metabolites and low coupling efficiency due to temperature disturbances can induce an imbalance in metabolism and affect the activity of cells (Fig. 3H).

4.3. HHP-induced peroxidation causes the metabolic shift

In recent studies, there are indications that HHP may induce significant metabolic alterations within cells, since it alters the intracellular oxidation status (Xie et al., 2017; Wang et al., 2020). HHP-induced peroxidation was suggested to play an important role in further influencing the shift of end products in fermentation and external electron acceptors in the respiratory chain. Yang et al. demonstrated that 3–25% of the methane consumed by ANME archaea is not completely oxidized to carbon dioxide but is converted to acetate via incomplete oxidation due to the impact of HHP (Yang et al., 2020). In addition to the change of end products in fermentation, the HHP also changes the aerobic respiration to the anerobic respiration in psychrophiles. Yin et al. isolated a piezosensitive marine bacterium under aerobic conditions. However, when it used anerobic respiration with the electron acceptor of trimethylamine N-oxide (TMAO) for energy metabolism, the same strain exhibited a piezophilic-like phenotype with optimal growth at 30 MPa (Yin et al., 2017). In addition, Li et al. found that the deep-sea piezophilic bacteria could perform nitrate respiration under HHP conditions, even in the presence of oxygen. It is not difficult to infer from the above clues that facultative aerobic microorganisms alter the anaerobic respiration under HHP to inhibit HHP-induced intracellular peroxidation (Fig. 3G).

Unfortunately, all the hints regarding metabolic shifts mentioned above are based on research in psychrophiles, and the scenarios in hyperthermophilic piezophiles remain unknown. Zhao et al. observed the cross-stress adaptation in a hyperthermophilic piezophile from deep-sea hydrothermal vent, including the responses to high temperature, HHP and other essential environmental parameters (i.e., cold, extreme pH and salinity), and revealed that potential shifts occurred to membrane-bound energetic complexes by utilizing different electron acceptors on proteomic level (Zhao et al., 2020). Vannier et al. also reported the overexpression of the cluster of genes encoding membrane-bound hydrogenases, which suggests switch of the energy metabolism towards a more pressure-efficient energy-harvesting mechanism to prevent pressure-induced proton transfer limitation through the membrane

(Vannier et al., 2015). Cario et al. observed 14 more amino acid requirements in a hyperthermophilic piezophile under HHP and hypothesized that the low energy yields of fermentation of organic polymers, together with energetic constraints imposed by high hydrostatic pressure, may render *de novo* synthesis of amino acids ecologically unfavorable (Cario et al., 2015). Regardless, it is still too early to draw conclusions on how high temperature and HHP impact metabolism, and systematic investigations of the interaction between these two factors are still insufficient, especially with respect to the quantitative analysis needed to shed light on how high temperature and HHP impact metabolism individually and how cooperatively.

5. Conclusions and prospects

Temperature is considered the key limit for life and habitat. The discovery of life in high-temperature environments in the deep sea, i.e., hydrothermal vents and deep subseafloor, profoundly extended our views of the boundary of both life and the habitat environments of the Earth. With the recognition of the significant impacts of HHP on cells, the way in which we view the physical, physiological, and metabolic profiles of life living in the deep sea and deep biosphere has also been changed. Despite the relatively clear and contrasting effects of high temperature and HHP on biological integrity, our knowledge of metabolic responses has many blind areas spots, even with respect to the individual stress of either high temperature or HHP, not to mention the mechanism of cross-stress adaptation. However, metabolism may provide a direct bridge between geochemistry and ecology. The current knowledge gaps regarding metabolism limit our understanding of the real microbiological functions mediating the elemental cycle under *in situ* polyextreme environments in the deep sea and hinder our estimation of where the boundaries for both life and habitats are located.

Based on the knowledges reviewed above during the exploration of the upper temperature limit of life and the correlation between high temperature and HHP, we raise a series of questions requiring further investigation: (1) Is there any convergent evolution in metabolism under high temperature and/or HHP; if so, which pathways (including both fermentation and respiration) are favorable? (2) What's the final effects under both high temperature and HHP? (3) Where is the real upper temperature limit of life, and which organism will hold the next record?

Declaration of competing interest

No conflict interests.

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