PERSPECTIVE





Functional groups in microbial ecology: updated definitions of piezophiles as suggested by hydrostatic pressure dependence on temperature

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Introduction

An environment is often best understood by the physiology of the organisms that inhabit it. In microbial ecology, the description of how microorganisms contribute to the functioning of their ecosystem is a daunting task, owing to their phylogenetic and physiological diversity, and our limited capacity to study them in their habitat, e.g., the deep sea. Categorization of microbes into functional groups that reflect either specific processes or habitat constraints is one approach to address this. However, this requires robust definitions of such groups. Where specialized structures or metabolic pathways exist, definition of such groups based on diagnostic genes or proteins is often possible. In contrast, where groups are to be defined based on habitat constraints for cell growth multidimensional stimuli must be considered, which is often challenging. The variation of hydrostatic pressure (HP), temperature (T), salinity, pH, oxygen availability, water activity, and radiation over evolutionary times contributed to shape the present microbial diversity, and still define the countless ecological niches on Earth. The biochemical adaptation to these different physicochemical stimuli may be similar (e.g., increase in unsaturated fatty acids [in

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Bacteria] or glycerol ether lipids [in Archaea] at high HP or low T; increase in ω -alicyclic fatty acids at high T or low pH; accumulation of polar organic solutes at low water activity or high T, HP, salinity or radiation; Mn²⁺ accumulation at high radiation or low water activity [1]). Nonetheless, some trade-offs exist which limit the capacity of microbes to grow under different combinations of conditions [2]. A clear definition of the operative boundaries imposed by such factors is key to the conceptual and practical use of functional groups. HP in the deep sea is one example.

HP is the force exerted on an area by a fluid at rest. The most pervasive effect of HP is its influence on intermolecular distances, where in addition to gas volumes it affects conformation of polynucleotides (DNA and RNA), lipid bilayers, and multimeric proteins [3]. Increased HP is experienced by planktonic crustaceans, and marine invertebrates, fish, and deep-diving mammals, and is characteristic of the largest microbial habitats on Earth i.e. the deep sea and subseafloor [4] where Bacteria and Archaea thrive at tens of MPa [5]. In food and medicine production, elevated HPs are managed to inactivate HP-sensitive pathogens and viruses [6]. However, a systematic categorization of microbial fitness constraints in response to HP is missing. Such preference is generally referred to as piezophily, descriptive of microorganisms growing better at increased HP, with obligate piezophiles (or hyperpiezophiles) unable to grow at ambient pressure, and piezosensitive strains growing best at ambient pressure. Although such simple concepts recognize the effect of HP on microbes, they do not yet provide a useful basis to truly define how HP gradients influence biogeochemical processes. At what depth are piezosensitive microorganisms outcompeted by piezophiles? Do such transitions shape the rates of key processes for ecosystem modeling? Are transition points similar in all water bodies or do they vary with other physicochemical properties such as T or salinity?

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HP linearly increases by 1 MPa every 100 m below seawater level (bswl), and about three times as much below seafloor level (bsfl) [3]. Enhanced growth at elevated HP has been used to locate the beginning of the piezosphere at corresponding depths (e.g. 1000 m bswl if HP was equal to the corresponding ~10 MPa). However, different HP thresholds were proposed for both piezophiles and hyperpiezophiles: ≥ 10 MPa [7]: ≥ 10 MPa for piezophiles and ≥ 50 MPa for hyperpiezophiles [8]; >0.1 MPa for piezophiles and ≥60 MPa for hyperpiezophiles [9], but indicating moderate piezophily if the HP optimum [HPopt] of an isolate under investigation was between 10 and 30 MPa [10]; ≥40 MPa (as the average oceans depth is ~3750 m bswl [11]). Following deep-sea sampling, isolation, and lab-scale testing, a seminal work by Yayanos in 1986 proposed that 'true' piezophiles populated waters at least 2000 m bswl (≥20 MPa). This work introduced the significant concept of PTk diagrams, where growth rates are plotted in threedimensional graphs versus HP and T. Such multidimensional space describing growth limits aligns well with the principle of ecological niches formalized by Hutchinson [12]. Defining piezophily by relationship between HP and growth rate is limited by the fact that other parameters (e.g. T) also impact growth rate. PTk diagrams provide a means to visualize the relationship between HP, T and growth rate, with the maximum growth rate $[\mu_{max}]$ observed when concomitantly adjusting HP and T to an optimum. Yayanos work was almost exclusively based on psychrophiles (microorganisms with a T optimum $[T_{opt}] \leq 15$ °C). The isolation of several new piezophiles in recent years, particularly with $T_{opt} > 15$ °C, is an opportunity to revise the role of T on the growth of piezophiles.

Deep-sea environments exposed to elevated HPs commonly experience low T (<5 °C). At polar regions, T decreases <5 °C already at ~100 m bswl, while at warmer low and middle latitudes T decreases rapidly along a permanent thermocline to $\sim 5 \,^{\circ}\text{C}$ at $\sim 1000 \,\text{m}$ bswl [13]. Exceptions are the deep, warm Sulu, Mediterranean, and Red Sea (~10, 13.5, and 20 °C at seafloor, respectively, at depths of ~4400, 5270, and 3040 m bswl). At hydrothermal vents as deep as 5800 m bswl (http://vents-data.interridge. org) microorganisms may grow >110 °C. In deep sub-seafloors, T increases 25 °C every km underground [9, 14]. Notwithstanding the many HP-T combinations in the environment, this correlation has not been systematically addressed. This lack of information can lead to a poor understanding of the true operative boundaries of a microorganism. For instance, thermophilic isolates collected from surface waters and theoretically belonging in that environment have shown to grow best at higher T when concomitantly increasing HP, in both Archaea (Methanococcus thermolithotrophicus [15]) and Bacteria (Clostridium paradoxum [16]).

Piezophiles separate in three functional groups based on T

To date, the most commonly accepted definition for piezophily states that piezophiles show a μ_{max} above the atmospheric pressure of 0.1 MPa. At the time of writing, there are only 86 documented microbial isolates with a $HP_{opt} > 0.1$ MPa, an incredibly small number for a condition featuring the largest reservoir of prokaryotes on the planet [4]. To determine if T exerts an ecologically-relevant effect on the relationship between HP and optimal growth rate, all $\mu_{\rm max}$ values in described piezophiles were plotted versus either HP_{opt} (Fig. S1A) or T_{opt} (Fig. S1B). This would explain growth based on HP or T independently of one another. High HP_{opt} is consistent with low μ_{max} while the opposite is true for Topt. However, no strict correlation appears evident. Piezophiles were then divided for T preference neglecting HPopt. Microbial preference for T does not result in subgroups with precise boundaries [17]. However, microorganisms with $T_{opt} \leq 15 \text{ }^{\circ}\text{C}$ are generally referred to as psychrophiles [18] and those with $T_{opt} \ge 50 \degree C$ as thermophiles [19], the resulting mesophiles having 16 < T_{opt} < 49 °C. The average μ_{max} in piezopsychro-, piezomeso- and piezothermophiles increases with T namely 0.22 ± 0.13 , 0.42 ± 0.38 and 1.25 ± 0.84 h⁻¹ (Table 1, all data in Table S1). Only the average μ_{max} in piezothermophiles is significantly different from the other groups (*t*-test, p < p0.0011). The opposite approach (i.e. neglecting T classification) was attempted using the HP thresholds suggested by Yayanos [9]: piezophiles >0.1 MPa up to 60 MPa; and hyperpiezophiles >60 MPa, however, no significant difference was found (p > 0.05, average μ_{max} equal to 0.55 ± 0.61 and $0.41 \pm 0.69 \text{ h}^{-1}$, respectively).

When accounting for the combined effects of HP and T on growth, a distinction of functional piezophilic groups emerges. Since both HP and T influence growth rate, the HP_{opt} and T_{opt} of every piezophile was divided by their μ_{max} to normalize the relationship across the available strains (Fig. 1). This revealed a correlation between HP and growth rate only when separating piezophiles in the three T-defined subgroups piezopsychro-, piezomesoand piezothermophiles, as it can be inferred by the large variations in the axes of Fig. 1. Within each subgroup, the normalized HP_{opt} and T_{opt} of all strains have an exponential correlation $(R^2 \text{ equal to } 0.62 \ (n = 37), 0.78 \ (n = 12) \text{ and } 0.58 \ (n = 17),$ respectively). The data points for Profundimonas piezophila YC-1 and Rhodobacterales bacterium PRT1 were removed from piezopsychrophiles, as they are the slowest piezophiles isolated so far $(\mu_{max} < 0.02 \text{ h}^{-1})$ and plot out of scale. Their inclusion increases R^2 from 0.62 to 0.87. For the same reason Archaeoglobus fulgidus VC-16^T was removed from piezothermophiles, its inclusion slightly reducing R^2 from 0.58 to 0.54.

N. Domain	Family	Strain	T growth rang (°C)	e T optimum (°C)	HP growth range (MPa)	HP optimum (MPa)	Capture depth (m)	Maximum growth rate (h ⁻¹)	Ref.	
A										
1 Bacteria	Shewanellaceae	Shewanella sp. SC2A	n.d.	2	0.1-42	7	1957	0.08	[25]	
2 Bacteria	Vibrionaceae	Photobacterium profundum DSJ4	4–18	10	0.1 - 70	10	5110	0.45	[33]	
4 Bacteria	I	Strain PE35	n.d.	2, unclear	0.1 - 83	14	3584	0.12	[25]	
7 Bacteria	Moritellaceae	Moritella sp. #304	n.d.	4	0.1 - 70	20	3064	0.31	[34]	
10 Bacteria	Vibrionaceae	Vibrio sp. WM145	1–22	2	0.1 - 82	27	4575	0.21	[26]	
16 Bacteria	Shewanellaceae	Shewanella benthica #302	n.d.	4	0.1 - 70	30	3064	0.35	[34]	
19 Bacteria	Moritellaceae	Moritella abyssi 2693 (T)	2–15. Min unclear	10	0.1–50	30	2815	0.2	[35]	
22 Bacteria	Moritellaceae	Moritella sp. strain PE36	0–12. Max unclear	10	0.1–70	41	3584	0.28	[20]	
25 Bacteria	Moritellaceae	Moritella sp. CT12	0-12	8	0.1 - 70	50	4819	n.d.	[36, 37]	
28 Bacteria	Psychromonadaceae	Psychromonas kaikoae JT7301 (T)	4–15. Max and Min unclear	10	10-70	50	7437	0.15	[38]	
31 Bacteria	Psychromonadaceae	Psychromonas sp. strain CNPT3	-2 to 15. Max unclear	12	0.1–85	52	5782	0.19	[39]	
34 Bacteria	Colwelliaceae	Colwellia piezophila Y251E (T)	n.d.	10	0.1 - 80	60	6278	n.d.	[40]	
37 Bacteria	Shewanellaceae	Shewanella benthica DB6705	4–15. Min unclear	15	0.1-70	60	6356	0.4	[41]	
40 Bacteria	Shewanellaceae	Shewanella benthica DB172F	n.d.	10	50 - 100	70	6499	0.41	[42]	
43 Bacteria	Moritellaceae	Moritella yayanosii DB21MT-5	n.d.	10	50 - 100	80	10898	0.2	[43]	
45 Bacteria	Colwelliaceae	Colwellia hadaliensis BNL-1	2–10. Max and Min unclear	10	37-102	90	7410	0.12	[44]	
48 Bacteria	Colwelliaceae	Colwellia marinimaniae MTCD1 (T)	4–10. Max and Min unclear	9	80-140	120	10918	0.08	[45]	
		Min	-5	2	0.1	7	Mean	0.22		
		Max	23	15	140	120	s.d.	0.13		
в										Relation to Oxygen
1 Bacteria	Alteromonadaceae	Salinimonas sediminis N102 (T)	4-40	28	0.1 - 70	10	4700	n.d.	[46]	Strictly aerobic
4 Bacteria	Rhodobacteraceae	Paraoceanicella profunda D4M1	10-45	37	0.1 - 70	10	10890	0.13	[47]	Aerobic
8 Bacteria	Vallitaleaceae	Petrocella atlantisensis 70B-A	10-35	25	n.d.	14	$1150 + 4^{*}$	0.45	[48]	Strictly anaerobic
11 Bacteria	Shewanellaceae	Shewanella piezotolerans WP3	0–28	15-20	0.1–50	20	1914	0.5	[49]	Facultatively anaerobic
14 Bacteria	Desulfovibrionaceae	Desulfovibrio hydrothermalis AM13 (T)	20-40	35	n.d.	26	2600	0.05	[50]	Strictly anaerobic
17 Bacteria	Dermacoccaceae	Dermacoccus abyssi MT1.1 (T)	10-37	28	n.d.	40	10898	n.d.	[51]	Aerobic
		Min	0	20	0.1	10	Mean	0.42		
		Max	70	45	70	40	s.d.	0.38		

. C J	undum lithotrophica 106	25-60	00	0.1 - 50	15	3626	0.30	[52]
Archaea Thermococcaceae Pyrococc	cus abyssi GE5	67-102	96	0.1 - 50	20	2000	0.98	[53]
Bacteria Clostridiaceae Clostridii	um paradoxum YL-7 (T)	30-70	60	0.1–30. Max unclear	22	0	3.50	[54, 16]
Archaea Thermococcaceae Thermoco A501 (T)	occus eurythermalis)	50-100	85	0.1 - 70	0.1 to 30	2000	1.25	[55]
Archaea Methanopyraceae Methanop	pyrus kandleri 116	80-122	105	0.1 - 50	40	2500	0.73	[56]
Archaea Thermococcaceae Thermoco 1 (T)	occus peptonophilus OG-	60-100	06	0.1 - 60	45	1380	1.38	[57, 30]
Archaea Methanocaldococcaceae Methano. JAL-1	caldococcus jannaschii	50–100 Min unclear	86	0.1–75	75	2610	2.36	[58]
Min		25	50	0.1	15	Mean	1.25	
Max		122	105	120	75	s.d.	0.84	

Keys to Table 1A,B,C: n.d. not determined, T temperature, HP hydrostatic pressure, (T) type strain, Ref. reference. Min and Max, and average and standard deviation (s.d.) values refer to the

complete list in Table S1. An asterisk indicates meters below seawater + meters below seafloor level.

SPRINGER NATURE

Fable 1 (continued)

Variations in T and HP can affect membrane fluidity (phospholipid fatty acids packing and conformation, affecting proton influx/efflux) and protein folding (structural disruption affecting activity). The subdivision of piezophiles into three functional T subgroups suggests that the evolutionary cellular adaptation to the constraints imposed by HP occurred within the boundaries of three subsets of T. However, the environment is not a two-dimensional space described by HP and T alone. Aside T [20], growth rates at increased HP may also depend on diversity and concentration of available nutrients [21], main carbon and energy substrate [7, 22], pH [23] and salinity [2]. For instance, variations in salinity in cold (e.g. Orca Basin, 5 °C), warm (e.g. Nereus Basin, 30 °C) and hot (e.g. Atlantis II Deep, up to 68 °C) deep brine pools (\sim 2400, 2500, and 2200 m bswl. respectively) may have additionally imposed a considerable water activity stress, affecting protein folding and turgor pressure. Cells maintain iso-osmosis with the environment by intracellular accumulation of salts (requiring the molecular adaptation of all intracellular enzymes) or organic compatible solutes (an energy-demanding strategy) [24]. Understanding how these halophiles' evolution has been constrained by concurrent HP and T boundaries requires a sizeable collection of isolates.

Estimating habitat preferences

The relationship between piezophiles' capture depth and HP_{opt} is reported (Fig. 2A). The almost linear correlation found with piezopsychrophiles ($R^2 = 0.69$, n = 48) may reflect their habitat, the contiguous cold seawaters where HP increases linearly to the seafloor (Fig. 2B, as derived from Figs. S2-S4). The small discrepancy between the linear increase in HP with capture depth (HP_{capt}) and HP_{opt} (dotted vs. straight line, Fig. 2A) indicates that in piezopsychrophiles $HP_{opt} < HP_{capt}$, consolidating previous observations on few isolates [25, 26]. As cold T and high HP impose similar constraints on cells [27], piezopsychrophiles may also inhabit permanently cold surface waters at polar regions $(-1.8 \text{ to } 5 \degree \text{C} [13];$ yellow lines, Fig. 2B). Piezomesophiles inhabit warm and deep anaerobic sediments up to ~2500 m bsfl. However, in 4/6 isolates collected underground HPopt«HPcapt (at least 2.4 times), suggesting that definition of piezomesophiles true maximum HPopt in sub-seafloors may require improved HP retainers. The warm, geographically limited seawaters of the Mediterranean, Sulu, and Red Sea (in orange, Fig. 2B) are another habitat for piezomesophiles, although rarely collected there (1/11, Table S1B). The irrelevant correlation between their capture depth and HP_{opt} ($R^2 = 0.03$, n = 11) highlights the high resilience of sinking piezomesophiles in colder, deeper seawaters ($HP_{capt} \ge HP_{opt}$ in 9/11) where they may compete with piezopsychrophiles. Similarly, high T



Fig. 1 Correlation between optimal HP and temperture with respect to maximum growth in piezophiles. The rate increase between HP_{opt} (HP_{opt}/ μ_{max}) and T_{opt} (T_{opt}/ μ_{max}) is described for piezopsychro- (**A**), piezomeso- (**B**), and piezothermophiles (**C**). Statistical correlation was obtained with GraphPad Prism 5, nonlinear regression, exponential growth equation, least square (ordinary) fit.

tolerant piezomesophiles (as those collected close to hydrothermal vents; 4/11, Table S1B) may compete with piezothermophiles. Piezothermophiles are mostly Archaea (15/21). No correlation between capture depth and HP_{opt} is evident ($R^2 = 0.07$, n = 21), even when removing the six Bacteria ($R^2 = 0.11$, n = 15). While piezothermophiles' most obvious habitat are deep hydrothermal vents (18/21, Table S1C; in red, Fig. 2B), those collected at hot vents have HP_{opt} > HP_{capt} (16/18), possibly because the cellular constraints imposed by high T can be compensated with increased HP [15, 16, 28–31].

Competitive advantage of piezophiles

The piezosphere is also inhabited by piezosensitive microorganisms [32]. The minimum HP setting a competitive advantage for piezophiles remains fairly unclear. The lowest HP_{opt} observed so far differs according to T: in



Fig. 2 Correlation between optimal HP and capture depth in piezophiles, and estimation of their habitat. In (A) the straight line indicates the linear regression for piezopsychrophiles ($R^2 = 0.69$, n =48) as obtained with GraphPad Prism 5, linear regression; the dotted line indicates the linear increase of HP with increasing depth in seawater: all data in Table S1. Keys reported in the graph. In (B) the global topography reporting oceans depth, surface temperature, and plate boundaries was obtained by over imposing three maps from the NOAA (National Center for Environmental Information; all data available in Supplementary Information). Keys: color scale for oceans seawater depth reported on the map as meters below seawater level (m bswl). Yellow lines indicate where surface temperature at polar seas is permanently <5 °C (data averaged from 1985 to 2010); thus, at low and mid latitude in between yellow lines surface temperature can be higher than 5 °C. Red lines indicate plate boundaries, where hydrothermal vents most commonly are found. Red dots indicate hydrothermal vents not on plate boundaries. The warm and deep Mediterranean, Sulu and Red Sea are highlighted in orange.

piezopsychrophiles, eight isolates have HP_{opt} between 10 and 20 MPa (except for *Shewanella* sp. SC2A at 7 MPa, whose growth rate is however almost identical until 14 MPa, 0.076 vs. $0.072 h^{-1}$, respectively [25]); in piezomesophiles, the lowest HP_{opt} is 10 MPa; in piezothermophiles it is 20 MPa (except for *Thioprofundum lithotrophica* 106 at 15 MPa). The present data thus suggests that at \ge 20 MPa piezophiles consistently possess a competitive advantage irrespective of T. This aligns with Yayanos' proposal on piezopsychrophiles [20]. None-theless, piezopsychro- and piezomesophiles may have an increasingly competitive advantage already ≥ 10 MPa. This may indicate that piezophiles could be collected from deep freshwater lakes as Lake Baikal and Tanganyika (1642 and 1470 m depth, respectively, at 16 and 14 MPa).

Hyperpiezophiles

Hyperpiezophiles are microorganisms that cannot grow at ambient pressure. There are several hyper-piezopsychrophiles (11/48), no isolated hyper-piezomesophiles, and just one isolated hyper-piezothermophile (*Pyrococcus yayanosii* CH1) (Table 1). The lowest HP_{opt} of hyper-piezopsychrophiles is 50 MPa (3/11 strains) and their shallowest capture depth is 6000 m bswl (Table S1), which aligns with the depth of abyssal plains. The fact that HP at the onset of abyssal plains is slightly higher than hyper-piezopsychrophiles' lowest HP_{opt} (~60 vs. 50 MPa) mirrors the small discrepancy noted for all piezopsychrophiles (Fig. 2A), overall indicating that hyper-piezopsychrophiles are autochthonous in deep, cold hadal trenches.

Updated definitions

The most widely shared definition of microbial preference for increased HP states that a microorganism is piezophilic when its μ_{max} is observed at HPs >0.1 MPa. By setting the threshold to such a low value, this definition neglects the large variation in HP preference among described piezophiles, and the differential effects enhanced HP may impose on the vast diversity of microbial processes in nature. Assessing optimal growth rates by cultivation is required to identify the exact threshold level above which HP-adapted microorganisms clearly separate from those thriving at ambient pressure. In the present meta-analysis, the relevance of HP–T combinations first described by Yayanos [20] was updated to include all currently described piezophiles. The following updated definitions and perspectives on their application are proposed:

(1) HP–T relationship constrains μ_{max} , and defines three functional groups based on T: piezopsychro-, piezomeso-, and piezothermophiles. These functional categories should be used to understand how piezophiles contribute to the functioning of deep-sea environments experiencing different HP–T combinations.

(2) Capture depth is a poor predictor of piezophilic traits, as piezosensitive and piezophilic groups are intermixed in the oceans.

3) A competitive advantage to piezophiles over piezosensitive is predicted to begin at 10 MPa and to consistently exist irrespective of T at HPs ≥ 20 MPa. Ecological modeling should specifically account for HP effects on biogeochemical processes beyond this point.

4) Hyper-piezopsychrophiles are autochthonous in hadal trenches. Their competitive advantage over piezo-psychrophiles begins at HP \ge 50 MPa. This threshold should be considered for ecological modeling of hadal trenches.

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Compliance with ethical standards

Conflict of interest The author declares no competing interests.

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References

- Capece MC, Clark E, Saleh JK, Halford D, Heinl N, Hoskins S, et al. Polyextremophiles and the constraints for terrestrial habitability. In: Seckbach J, Oren A, Stan-Lotter H, editors. Polyextremophiles. Life under muliple forms of stress. Dordrecht, Neaderlands: Springer; 2013. p. 3–60.
- Harrison JP, Gheeraert N, Tsigelnitskiy D, Cockell CS. The limits for life under multiple extremes. Trends Microbiol. 2013;21:204–12.
- Oger PM, Jebbar M. The many ways of coping with pressure. Res Microbiol. 2010;161:799–809.
- Whitman WB, Coleman DC, Wiebe WJ. Prokaryotes: the unseen majority. Proc Natl Acad Sci USA. 1998;95:6578–83.
- Bartlett DH. Pressure effects on in vivo microbial processes. Biochim Biophys Acta. 2002;1595:367–81.
- Aertsen A, Meersman F, Hendrickx ME, Vogel RF, Michiels CW. Biotechnology under high pressure: applications and implications. Trends Biotechnol. 2009;27:434–41.
- Jannasch HW, Taylor CD. Deep-sea microbiology. Ann Rev Microbiol. 1984;38:487–514.
- Fang J, Zhang L, Bazylinski DA. Deep-sea piezosphere and piezophiles: geomicrobiology and biogeochemistry. Trends Microbiol. 2010;18:413–22.
- Yayanos AA. Microbiology to 10,500 meters in the deep sea. Ann Rev Microbiol. 1995;49:777–805.
- Eloe EA, Lauro FM, Vogel RF, Bartlett DH. The deep-sea bacterium *Photobacterium profundum* SS9 utilizes separate flagellar systems for swimming and swarming under high-pressure conditions. Appl Environ Microbiol. 2008;74:6298–305.
- Horikoshi K, Bull AT Prologue: Definition, categories, distribution, origin and evolution, pioneering studies, and emerging fields of extremophiles. In: Horikoshi K, editor. Extremophiles handbook. Tokyo, Japan: Springer; 2011. p. 3–18.
- Holt RD. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proc Natl Acad Sci USA. 2009;106:19659–65.
- Talley LD, Pickard GL, Emery WJ, Swift JH. Typical distributions of water characteristics. In: Descriptive physical oceanography, 6th ed. London, UK: Elsevier; 2011. p. 67–110.
- Jebbar M, Franzetti B, Girard E, Oger P. Microbial diversity and adaptation to high hydrostatic pressure in deep-sea hydrothermal vents prokaryotes. Extremophiles. 2015;19:721–40.
- 15. Berhardt G, Jaenicke R, Ludemann H-D, Konig H, Stetter KO. High pressure enhances the growth rate of the thermophilic

archaebacterium *Methanococcus thermolithotrophicus* without extending its temperature range. Appl Environ Microbiol. 1998;54:1258–61.

- Scoma A, Garrido-Amador P, Nielsen SD, Roy H, Kjeldsen KU. The polyextremophilic bacterium *Clostridium paradoxum* attains piezophilic traits by modulating its energy metabolism and cell membrane composition. Appl Environ Microbiol. 2019;85: e00802–19.
- Wiegel J. Temperature spans for growth: hypothesis and discussion. FEMS Microbiol Rev. 1990;75:155–70.
- Morita RY. Psychrophilic bacteria. Bacteriol Rev. 1975;39:144–67.
- Zeikus JG. Thermophilic Bacteria—Ecology. Physiol Technol Enz Microb Technol. 1979;1:243–52.
- Yayanos AA. Evolutional and ecological implications of the properties of deep-sea barophilic bacteria. Proc Natl Acad Sci USA. 1986;83:9542–6.
- 21. Jannasch HW, Wirsen CO. Variability of pressure adaptation in deep sea bacteria. Arch Microbiol. 1984;139:281–8.
- 22. Yayanos AA, Chastain R. The influence of nutrition on the physiology of piezophilic bacteria. In: Bell CR, Brylinsky M, Johnson-Green P, Eds. Proceedings of the 8th International Symposium on Microbial Ecology. Halifax, NS, Canada: Atlantic Canada Society for Microbial Ecology; 6; 1999.
- Matsumura P, Keller DM, Marquis RE. Restricted pH ranges and reduced yields for bacterial growth under pressure. Microb Ecol. 1974;1:176–89.
- Oren A. Bioenergetic aspects of halophilism. Microbiol Mol Biol Rev. 1999;63:334–48.
- Yayanos AA, Dietz AS, Van, Boxtel R. Dependence of reproduction rate on pressure as a hallmark of deep-sea bacteria. Appl Environ Microbiol. 1982;44:1356–61.
- Deming JW, Hada H, Colwell RR, Luehrsen KR, Fox GE. The ribonucleotide sequence of 5S rRNA from two strains of deep-sea barophilic bacteria. J Gen Microbiol. 1984;130:1911–20.
- Lauro FM, Chastain RA, Blankenship LE, Yayanos AA, Bartlett DH. The unique 16S rRNA genes of piezophiles reflect both phylogeny and adaptation. Appl Environ Microbiol. 2007;73:838–45.
- Marteinsson VT, Birrien J-L-, Reysenbach A-L, Vernet M, Marie D, Gambacorta A, et al. *Thermococcus barophilus* sp. nov., a new barophilic and hyperthermophilic archaeon isolated under high hydrostatic pressure from a deep-sea hydrothermal vent. Int J Syst Bacteriol. 1999;49:351–9.
- Alain K. Marinitoga piezophila sp. nov., a rod-shaped, thermopiezophilic bacterium isolated under high hydrostatic pressure from a deep-sea hydrothermal vent. Int J Sys Evol Microbiol. 2002;52:1331–9.
- Canganella F, Gonzalez JM, Yanagibayashi M, Kato C, Horikoshi K. Pressure and temperature effects on growth and viability of the hyperthermophilic archaeon *Thermococcus peptonophilus*. Arch Microbiol. 1997;168:1–7.
- Canganella F, Gambacorta A, Kato C, Horikoshi K. Effects of hydrostatic pressure and temperature on physiological traits of *Thermococcus guaymasensis* and *Thermococcus aggregans* growing on starch. Microbiol Res. 2000;154:297–306.
- Tamburini C, Boutrif M, Garel M, Colwell RR, Deming JW. Prokaryotic responses to hydrostatic pressure in the ocean-a review. Environ Microbiol. 2013;15:1262–74.
- Nogi Y, Masui N, Kato C. Photobacterium profundum sp. nov., a new, moderately barophilic bacterial species isolated from a deepsea sediment. Extremophiles. 1998;2:1–7.
- Arakawa S, Nogi Y, Sato T, Yoshida Y, Usami R, Kato C. Diversity of piezophilic microorganisms in the closed ocean Japan Sea. Biosci Biotechnol Biochem. 2006;70:749–52.
- 35. Xu Y, Nogi Y, Kato C, Liang Z, Ruger H-J, De Kegel D, et al. Moritella profunda sp. nov. and Moritella abyssi sp. nov., two

psychropiezophilic organisms isolated from deep Atlantic sediments. Int J Syst Evol Microbiol. 2003;53:533-8.

- Sekiguchi T, Sato T, Enoki M, Kanehiro H, Kato C. Procedure for isolation of the plastic degrading piezophilic bacteria from deepsea environments. J Jap Soc Extremophil. 2010a;9:25–30.
- Sekiguchi T, Sato T, Enoki M, Kanehiro H, Uematsu K, Kato C. Isolation and characterization of biodegradable plastic degrading bacteria from deep-sea environments. JAMSTEC Rep. Res Dev. 2010b;11:33–41.
- Nogi Y, Kato C, Horikoshi K. Psychromonas kaikoae sp. nov., a novel piezophilic bacterium from the deepest cold-seep sediments in the Japan Trench. Int J Syst Evol Microbiol. 2002;52:1527–32.
- Yayanos AA, Dietz AS, van Boxtel R. Isolation of a deep-sea barophilic bacterium and some of its growth characteristics. Science. 1979;205:808–10.
- Nogi Y, Hosoya S, Kato C, Horikoshi K. Colwellia piezophila sp. nov., a novel piezophilic species from deep-sea sediments of the Japan Trench. Int J Syst Evol Microbiol. 2004;54:1627–31.
- Kato C, Sato T, Horikoshi K. Isolation and properties of barophilic and barotolerant bacteria from deep-sea mud samples. Biodiv Cons. 1995;4:1–9.
- Kato C, Inoue A, Horikoshi K. Isolating and characterizing deepsea marinemicroorganisms. Tibtech. 1996;14:6–12.
- Nogi Y, Kato C. Taxonomic studies of extremely barophilic bacteria isolated from the Mariana Trench and description of Moritella yayanosii sp. nov., a new barophilic bacterial isolate. Extremophiles. 1999;3:71–7.
- 44. Deming JW, Somers LK, Straube WL, Swartz DG, Macdonell MT. Isolation of an Obligately Barophilic Bacterium and Description of a New Genus, Colwellia gen. nov. Systematic and Applied Microbiology. 1988;10:152–60.
- 45. Kusube M, Kyaw TS, Tanikawa K, Chastain RA, Hardy KM, Cameron J, et al. Colwellia marinimaniae sp. nov., a hyperpiezophilic species isolated from an amphipod within the Challenger Deep, Mariana Trench. Int J Syst Evol Microbiol. 2017;67:824–31.
- 46. Cao J, Lai Q, Liu P, Wei Y, Wang L, Liu R, et al. Salinimonas sediminis sp. nov., a piezophilic bacterium isolated from a deepsea sediment sample from the New Britain Trench. Int J Syst Evol Microbiol. 2018;68:3766–71.
- 47. Liu P, Ding W, Lai Q, Liu R, Wei Y, Wang L, et al. Physiological and genomic features of Paraoceanicella profunda gen. nov., sp. nov., a novel piezophile isolated from deep seawater of the Mariana Trench. MicrobiologyOpen. 2019;00:e966.
- 48. Quéméneur M, Erauso G, Frouin E, Zeghal E, Vandecasteele C, Ollivier B, et al. Hydrostatic Pressure Helps to Cultivate an Original Anaerobic Bacterium From the Atlantis Massif Subseafloor (IODP Expedition 357): Petrocella atlantisensis gen. nov. sp. nov. Front Microbiol. 2019;10:1497.
- Xiao X, Wang P, Zeng X, Bartlett DH, Wang F. Shewanella psychrophila sp. nov. and Shewanella piezotolerans sp. nov., isolated from west Pacific deep-sea sediment. Int J Syst Evol Microbiol. 2007;57:60–5.
- Alazard D, Dukan S, Urios A, Verhe F, Bouabida N, Morel F, et al. Desulfovibrio hydrothermalis sp. nov., a novel sulfatereducing bacterium isolated from hydrothermal vents. Int J Syst Evol Microbiol. 2003;53:173–8.
- Pathom-Aree W, Nogi Y, Sutcliffe IC, Ward AC, Horikoshi K, Bull AT, et al. Dermacoccus abyssi sp. nov., a piezotolerant actinomycete isolated from the Mariana Trench. Int J Syst Evol Microbiol. 2006;56:1233–7.
- 52. Takai K, Miyazaki M, Hirayama H, Nakagawa S, Querellou J, Godfroy A. Isolation and physiological characterization of two novel, piezophilic, thermophilic chemolithoautotrophs from a deep-sea hydrothermal vent chimney. Environ Microbiol. 2009;11 (8):1983–97.

- Erauso G, Reysenbach A-L, Godfroy A, Meunier J-R, Crump B, Partensky F, et al. Pyrococcus abyssi sp. nov., a new hyperthermophilic archaeon isolated from a deep-sea hydrothermal vent. Arch Microbiol. 1993;160:338–49.
- Li Y, Mandelco L, Wiegel J. Isolation and Characterization of a Moderately Thermophilic Anaerobic Alkaliphile. Clostridium paradoxum sp. nov. Int J Sys Bacteriol. 1993;43:450–60.
- 55. Zhao W, Zeng X, Xiao X. Thermococcus eurythermalis sp. nov., a conditional piezophilic, hyperthermophilic archaeon with a wide temperature range for growth, isolated from an oil-immersed chimney in the Guaymas Basin. Int J Sys Evol Microbiol. 2015;65:30–5.
- 56. Takai K, Nakamura K, Toki T, Tsunogai U, Miyazaki M, Miyazaki J, et al. Cell proliferation at 122 degrees C and isotopically heavy CH4 production by a hyperthermophilic methanogen under high-pressure cultivation. Proc Natl Acad Sci U S A. 2008;105:10949–54.
- González JM, Kato C, Horikoshi K. Thermococcus peptonophilus sp. nov., a fast-growing, extremely thermophilic archaebacterium isolated from deep-sea hydrothermal vents. Arch Microbiol. 1995;164:159–64.
- Jones WJ, Leigh JA, Mayer F, Woese CR, Wolfe RS. Methanococcusjannaschii sp. nov., an extremely thermophilic methanogen from a submarine hydrothermal vent. Arch Microbiol. 1983;136:254–61.