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Review

Extremophiles for microbial-electrochemistry applications: A critical review

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ABSTRACT

Extremophiles, notably archaea and bacteria, offer a good platform for treating industrial waste streams that were previously perceived as hostile to the model organisms in microbial electrochemical systems (MESs). Here we present a critical overview of the fundamental and applied biology aspects of halophiles and thermophiles in MESs. The current study suggests that extremophiles enable the MES operations under a seemingly harsh conditions imposed by the physical (pressure, radiation, and temperature) and geochemical extremes (oxygen levels, pH, and salinity). We highlight a need to identify the underpinning mechanisms that define the exceptional electrocatalytic performance of extremophiles in MESs.

1. Introduction

Extremophiles can survive as well as thrive in harsh conditions imposed by physical (pressure, radiation, and temperature) and geochemical extremes (desiccation, oxygen levels, pH, salinity and redox potential) that challenge the typical functions of life (Gerday & Glansdorff, 2007; Singh, 2012; Stan-Lotter & Fendrihan, 2012). The definition of an extremophile often varies and it depends upon the perspective of the reader (e.g., anthropocentric, ecological and philosophical perspectives) (Rothschild & Mancinelli, 2001). Nevertheless, it has been unanimously agreed that extremophiles live in a variety of harsh physiological conditions including subzero temperatures (glaciers) as well as the boiling conditions (volcanoes) (Stan-Lotter & Fendrihan, 2012) (Table 1).

In our earlier studies, we have demonstrated that thermophiles live in the deep mine tunneling environments of the Sanford Underground Research Laboratory (SURF) at a depth of 2000 feet where the temperature can reach as high as 100 ^{O}F. The SURF is an abandoned gold mine in the South Dakota state, which is currently being used as the deep underground facility for carrying out dark matter and neutrino experiments. Our recent reports have provided details about the extremophiles that exist in the SURF environments (Rastogi et al., 2009; Rastogi et al., 2010; Singh et al., 2017). Extremophiles have been reported to live in deep biospheres, hot springs, and saline water bodies.

Extremophiles can be used to develop a range of commercial products in agriculture, mining, nanotechnology, and other industrial sectors. To identify the types of extremophiles that have been recently implemented in microbial electrochemical systems (MESs), we have searched seven popular databases including Scopus, Elsevier, Google scholar, National Center for Biotechnology Information, PubMed NCBI, Google.com, world cat, using the six keywords (extremophiles, thermophiles, halophiles, high temperature microbes, high salt microbes, and MESs). The search process indicated that 68% of the extremophile-based MESs were based on halophiles and thermophiles (Supplementary Fig. S1). Fig. 1 depicts an overview of the physical limits tolerated by the thermophiles and halophiles, respectively. Table 2 provides relevant examples of the thermophiles and halophiles that were previously isolated from Dead Sea, SURF, and Yellow stone national park.

Here we provide a critical overview of the fundamental and applied aspects of the MES studies (through November 2017) based on halophiles and thermophiles. The reader is suggested to review the recent literature to gain an understanding about other extremophiles (acidophiles, alkaliphiles psycrophiles, piezophiles, and xerophiles) in the MES applications (Dopson et al., 2016). First, we present an overview of halophiles and thermophiles in MESs. Next, we discuss the survival mechanisms used by these two extremophiles (Figs. 2, 3). The remaining part of the study will focus on the: (1) potential applications of halophiles and thermophiles in MESs; (2) knowledge gaps related to electrocatalysis and extracellular electron transfer mechanisms of halophiles and thermophiles; (3) and potential engineering challenges posed by hot and hypersaline electrolytes. Due to the limited and

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Table 1
Classification and examples of extremophiles.

Environmental parameter	Type	Definition	Examples
Chemical extreme	Gases Metals	Tolerates high level of metal	*C. caldarium* (pure CO_2) *Ferroplasma acidarmanus* (Cu, As, Cd, Zn)
Desiccation	Xerophiles	Anhydrobiotic	*Artemia salina*, Nematodes, Microbes, Fungi, Lichens
Gravity	Hypergravity	$> 1g$	Unknown
	Hypogravity	$> 1g$	Unknown
Oxygen tension	Anaerobe	Does not require oxygen	*Methanococcus jannaschii*
	Microaerophile	Tolerates some oxygen	*Clostridium*
	Aerobe	Requires oxygen	*H. sapiens*
pH	Alkaliphile	pH > 9	Natronobacterium, *Bacillus firmus* OF4, *Spirulina* spp. (all pH 10.5)
	Acidophile	Low pH loving	*Cyanidium caldarium,* *Ferroplasma sp.* (both pH 0)
Pressure	Barophile	Weight-loving	Unknown
	Piezophile	Pressure-loving	*Desulfuromonas acetoxidans*
Radiation	–	–	*Deinococcus radiodurans*
Salinity	Halophile	Salt-loving (2–5 M NaCl)	Halobacteriaceae, *Dunaliella salina*
Temperature	Hyperthermophile	> 80 °C	*Pyrolobus fumarii*, 113 °C
	Thermophile	60–80 °C	*Synechococcus lividis*
	Mesophile	15–60 °C	Homo sapiens
	Psychrophile	< 15 °C	*Psychrobacter*
Vacuum		Tolerates vacuum	Tardigrades, Insects

Adapted from (Rothschild & Mancinelli, 2001).

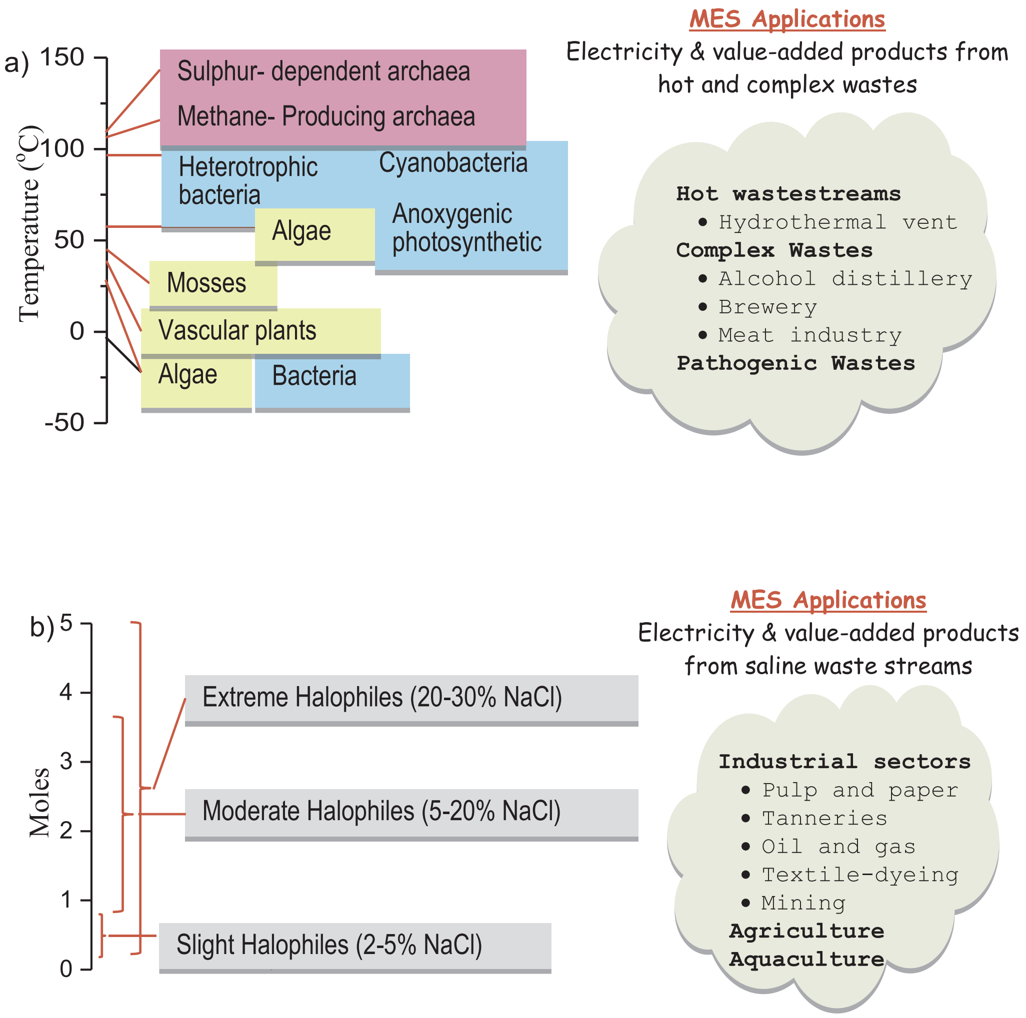

Fig. 1. Physical limits for select extremophiles and potential benefits of extremophiles a) Thermophiles (temperature limits) b) Halophiles (salinity ranges). *Notes:* MESs-Microbial electrochemical systems Physical Limits adapted from (Rothschild & Mancinelli, 2001; Crowley, 2017).

Table 2
Novel thermophiles and halophiles isolated from Sanford underground research laboratory (SURF) and Yellowstone national park in the United States and from other parts of the world.

S.N	Strain	Source	Benefit
	Thermophile		
1	*Geobacillus* sp. strain GHH01	Botanischer Garten, Germany	Produces extracellular thermostable lipases
2	*Geobacillus* sp. isolate T6	Thermal spring, Argentina	Possesses 878 enzyme-coding genes of potential application on agriculture, environment, biosensor, biotechnology, medicine, biofuel, food, and other industries
3	*Geobacillus thermopakistaniensis* strain MAS1	Hot spring, Pakistan	Possesses unique combination of glycosyl hydrolases genes and other industrially important enzymes
4	*Geobacillus* sp. Strain WSUCF1	Compost facility, United States	Produces highly thermostable lignocellulose deconstruction enzymes when grown on lignocellulosic substrates (e.g. corn stover, prairie cord grass) Useful for biofuel production processes
5	*Geobacillus thermodenitrificans* DSM 101,594	Compost facility, Lithuania	Possesses number of genes encoding enzymes of potential biotechnological importance
6	*Geobacillus* sp. Strain Sah69	Hot Saharan soil, Algeria	Potential sources of novel enzymes, such as those involved in the degradation of recalcitrant polymers
7	*Geobacillus* sp. Strain FW23	Mehsana oil wells, India	Possesses genes encoding enzymes involved in the degradation of aromatic and aliphatic compounds such as toluene, xylene, naphthalene, dichlorobenzene, bromobenzene, dichloroethylene, and trichloroethylene
8	*Geobacillus stearothermophilus* Strains 22 and 53	Garga hot spring, Russia	Contains active enzymes in ionic liquid and is a promising method for pretreatment of lignocellulosic biomass
9	*Geobacillus* sp. Strains AMR5420 and CAMR12739	Skaltholt, Iceland	Degrades plant cell wall hemicellulose polymers into their component pentose sugars
10	*Geobacillus stearothermophilus*	Evaporator in a milk powder manufacturing plant, New Zealand	Adapts to specific environment such as milk powder manufacturing plants
11	*Geobacillus* sp. Strain ZGt-1	Zara hot spring, Jordan	Produces antimicrobial peptide
12	*Geobacillus sp.* 44B	SURF, United States	Produces high level of extracellular cholesterol oxidase
13	*Geobacillus sp.* 44C	SURF, United States	Adapts to significant evolutionary pressures exerted by its naturally inhospitable conditions (hot, dark, and deep subsurface)
14	*Geobacillus sp.* 46C-IIa	SURF, United States	Adapts to significant evolutionary pressures exerted by its naturally inhospitable conditions (hot, dark, and deep subsurface)
15	*Geobacillus sp.* 47C-IIb	SURF, United States	Adapts to significant evolutionary pressures exerted by its naturally inhospitable conditions (hot, dark, and deep subsurface)
16	*Geobacillus thermocatenulatus*	SURF, United States	Adapts to significant evolutionary pressures exerted by its naturally inhospitable conditions (hot, dark, and deep subsurface)
17	*Geobacillus thermocatenulatus*	SURF, United States	Adapts to significant evolutionary pressures exerted by its naturally inhospitable conditions (hot, dark, and deep subsurface)
18	*Geobacillus thermocatenulatus*	SURF, United States	Adapts to significant evolutionary pressures exerted by its naturally inhospitable conditions (hot, dark, and deep subsurface)
	Halophile		
19	*Halogeometricum borinquense* type strain (PR3T)	Solar salterns of Cabo Rojo, Puer-to Rico	Grows aerobically and anaerobically (using nitrate as electron acceptor) in extremely high salt conditions
20	*Halomicrobium mukohataei* type strain (arg-2 T)	Alinas Grandes in Jujuy, Argentina	Grows essentially aerobically, but can also grow anaerobically under a change of morphology and with nitrate as electron acceptor
21	*Chromohalobacter salexigens* type strain (1H11T)	Netherlands Antilles	Synthesizes of ectoines (ectoine and hydroxyectoine) for cell stress protection
22	*Haloarcula marismortui, Natrialba asiatica, Halorubrum lacusprofundi, Halobaculum gomorrense*	Solar saltern facilities, the Dead Sea coast	Exhibits both bacterial and eukaryotic characteristics as well as uniquely archaeal traits
23	*Hahella chejuensis*	Coastal marine sediment, South Korea	Helps in mitigation of algal blooms, genetic make-up, physiology, biotic interactions and biological roles in the community of a marine bacterium
24	*Haloarcula marismortui*	Dead Sea	Adapts to an acidic proteome of average isoelectric point of 4.5 Lives in an organic-rich environment and extreme environment (high or low oxygen concentrations, harsh radiation, and the potential for desiccation
25	*Halorhodospira halophila* SL1	Oregon, United States	Grows at photoautotrophic extreme conditions Capable of sulfur metabolism.
26	*Chromohalobacter salexigens*	Bonair, Netherlands Antilles	Functions at high salt concentration and contains highly acidic proteins
27	*Halanaeroarchaeum sulfurireducens*	Altai, Russia	Grows exclusively by sulfur respiration
28	*Mobilitalea sibirica*	Siberia, Russia	Ferments variety of mono-, di- and polysaccharides, including microcrystalline cellulose

Note: SURF –Sanford underground research facility; Adapted from (Alkhalili et al., 2015; Baliga et al., 2004; Bezuidt et al., 2015; Bhalla et al., 2013; Burgess et al., 2015; Challacombe et al., 2013; Copeland et al., 2011; De Maayer et al., 2014; Goo et al., 2004; Jeong et al., 2005; Malfatti et al., 2009; Oren et al., 2005; Ortiz et al., 2015; Petkauskaite et al., 2017; Podosokorskaya et al., 2014; Pore et al., 2014; Rozanov et al., 2014; Rozanov et al., 2015; Siddiqui et al., 2014; Singh et al., 2017; Sorokin et al., 2016; Tindall et al., 2009; Wiegand et al., 2013).

delayed availability of R&D studies on the specific defense strategies used by the extremophiles in MESs, we limit our discussion to the survival strategies exhibited by the extremophiles in the natural environments.

2. Overview of MES, halophiles, and thermophiles

MESs enable interactions between living cells and electrodes or capacitive materials for generating electricity, energy carriers (hydrogen and methane), or chemicals (chlorine and sodium hydroxide) from organic matter. MES is represented by an "MXC" where X stands for an application of interest. F in MFC stands for fuel cell, where MFC is a microbial fuel cell. Other MXCs include microbial desalination cells (MDCs), microbial electrolysis cells (MECs), and microbial capacitive deionization cells (MCDCs). They can be used for treating the waste streams, as well as for pretreating or polishing the effluents from anaerobic digestion, membrane bioreactor, and membrane filtration technologies (Dai et al., 2017). We encourage the readers to review the recent literature to get an insight on the state-of-the art MESs (Gude et al., 2013; Harnisch & Schröder, 2010; Logan, 2010; Logan & Rabaey, 2012; Pant et al., 2011; Pant et al., 2010; Wang & Ren, 2013). The MESs can also be integrated with phototrophic microorganisms to develop

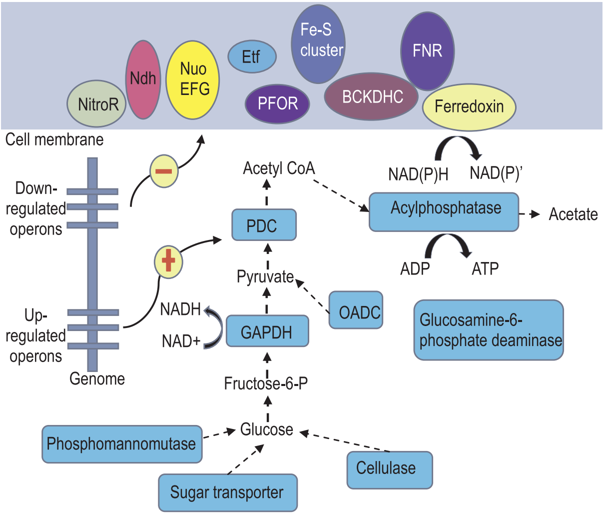

Fig. 2. Schematic illustrates the energy-generation processes of *T. tengcongensis* in response to increasing temperatures. *Notes:* **Rectangular box**-Upregulated proteins in response to an increase in the growth temperature. They are located in the cytoplasm and they are involved in glycolysis and the related pathways. **Elliptical box**-Downregulated proteins in response to an increase in the temperature. They are associated with the membrane and they are involved in the sulfur respiration. **NitroR**-nitroreductase; **Ndh**-NADH dehydrogenase FAD-containing subunit; **Nuo EFG**-NADH dehydrogenase/NADH:ubiquinone oxidoreductase subunit E/F/G; **Etf**-electron transfer flavoprotein; **PFOR**-pyruvate:ferredoxin oxidoreductase and related 2-oxoacid:ferredoxin oxidoreductase; **Fe-S Cluster**-Fe-S-cluster-containing hydrogenase; **BCKDHC**-branched-chain alpha-keto acid dehydrogenase complex; **FNR**-ferredoxin-NADP(H) reductase; **APDH**-glyceraldehyde-3-phosphate dehydrogenase; **OADC**-oxaloacetate decarboxylase; **PDC**-pyruvate dehydrogenase complex. **NADP**-Nicotinamide adenine dinucleotide phosphate. Adapted from (Wang et al., 2015).

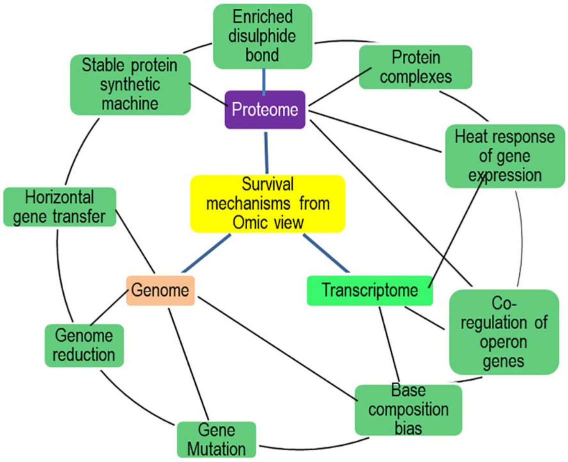

Fig. 3. A summary of the coordinative network of the study of the survival mechanisms of thermophiles using omics approaches. *Notes:* **Genomics studies**-Demonstrates thermal tolerance depends on heritable variations such as genomic size shrinkage, horizontal DNA transfer, and gene mutation **Gene expression in the transcriptome and proteome**-Illustrates that global transcriptional regulation of key functional genes is an efficient method for responding to increasing temperatures. **Proteomics evidence**-Demonstrates that thermophiles contain gene clusters that encode thermostable proteins. Thermophiles have pivotal functions for living cells, including proteins in the heat shock proteins family, glycolysis pathway, antioxidants, and antitoxins. Adapted from (Wang et al., 2015).

photosynthetic applications (ElMekawy et al., 2014; Gajda et al., 2013; Rosenbaum et al., 2010; Xiao & He, 2014). The biology of photosynthetic microorganisms in MESs has been well documented in the recent literature (de-Bashan et al., 2008; Gonzalez et al., 2009; Morita et al., 2000; Pan et al., 2011). The recent literature provides a deeper understanding on the role of photosynthetic microbes in the MESs (Barnard et al., 2010; Pikuta & Hoover, 2004; Tiwari & Pandey, 2012).

Recent studies have shed a light on the molecular mechanisms used by the halophiles for protecting their proteins under the saline conditions (DasSarma & DasSarma, 2015; Yin et al., 2015). These findings pave a path for using the halophiles in MESs for treating recalcitrant waste streams including produced water generated during the fracturing of the tight oil shales. The produced water is characterized by a range of xenobiotic compounds (biocides, organic solvents, and corrosion inhibitors), detritus of the fractured well (naturally occurring radioactive materials), and unusually high levels of dissolved solids (220,000 mg L^{-1}) (Shrestha et al., 2017a), reducing its amenability in typical biological processes. Our recent study suggest that microbial fuel cells and microbial capacitive deionization cells can treat produced water from the Bakken shale (Shrestha et al., 2018). The use of halophiles in MESs can increase the options for treating hypersaline wastewater streams that account for nearly 5% of the worldwide effluents (Grattieri et al., 2017). MESs are yet to be explored as alternatives to membrane separation and ion exchange processes currently used for treating saline streams from tanning, textile dyeing, pulp and paper production, and mining (Details of halophile-based MESs in Section 5). On the other hand, thermophiles are beneficial for treating lignocellulosic substrates, along with the benefits related to enhanced electrocatalysis rates, reduced mass transfer limitations, and improved ability to inhibit pathogens.

2.1. Electrocatalytic activity of extremophiles

A majority of the reported studies attribute the enhanced electrocatalytic of extremophiles to their ability to live under extreme physiological conditions (e.g., high temperatures) that enhance the electrocatalytic kinetics (Supplementary Table S1). For example, in a study by Parameswaran et al. (2013), it has been reported that *Thermincola ferriacetica* offers high current density (8 A/m^2) when compared with the MESs studies based on the mesophiles. The enhanced electroactivity of this thermophile has been attributed to the operating variables related to the temperature (60 °C); electrodes with enhanced surface properties; and efficient catalysts. However, it is not clear if the unique biological machinery of the thermophiles contribute to the improved electrocatalytic activity.

2.2. Unique membrane structure in thermophiles and halophiles

Extremophiles adapt to the challenging physiological conditions by modifying their membrane structure. Thermophiles respond to changes in external temperature by modifying its cytoplasmic membrane lipid composition (Koga, 2012; van de Vossenberg et al., 1998). The membrane structure of thermophiles has been reported to be characterized by a unique lipid structure based on ether lipids, ester lipids, tetraether lipids, diethertype polar lipids, and isofatty acids (Koga, 2012). For example, the fatty acid composition of the membranes in *Clostridia* has been reported to be associated with higher content of the saturated lipids including straight chain and branched-chain fatty acids (Chan et al., 1971). In contrast, the membranes in the mesophiles and psychrophiles are solely based on the unsaturated fatty acids. Details on the membrane structure of the thermophiles have been documented in the literature (Meruelo et al., 2012; Zeldovich et al., 2007).

Halophiles deal with the osmotic stress by modifying their membrane systems to pump the potassium into the cell while pumping the sodium out of the cell (Reed et al., 2013). The lipid constituents in their membranes have been reported to be based on the hydrocarbon substituents saturated phytanyl groups linked by ether bonds to glycerol carbons 2 and 3 (Quinn et al., 1986); and the lipid structure was highly charged and hydrated with polar head groups. The membranes in the extremely halophilic Archaea are characterized by the abundance of a diacidic phospholipid, archaetidylglycerol methyl phosphate, accounting for 50–80 mol% of the polar lipids. Further, they are characterized by the absence of phospholipids with choline, ethanolamine, inositol, and serine head groups (Tenchov et al., 2006).

We highlight the need for studies to investigate if the unique membrane structures in the halophiles (or thermophiles) contribute to the bio-electrocatalysis in MESs. It is currently unknown if the membrane structure in the halophiles (or thermophiles) can enhance the mass transfer characteristics of the solutes (electron donors and electron acceptors) across the membrane; electrocatalytic rates; expression of electron transfer proteins; and the electron transfer kinetics in MESs.

3. Survival mechanisms

Extremophiles belonging to archaea, bacteria, and eukarya use similar strategies to thrive under harsh conditions, specifically by secreting a range of indigenous metabolic products (extremolytes), extremozymes, and primary and secondary products. The secreted products allow the proteins to adapt their conformations and motions in response to the stressful conditions (Babu et al., 2015).

3.1. Defense mechanisms of thermophiles

Fig. 2 depicts an overview of the processes used by *Thermoanaerobacter tengcongensis* sp. to survive under hot conditions. They use the following sequential steps: activate the transcriptional regulators of the gene clusters of sulfur respiration and glycolysis; form an inverse coordination network in gene expression; attenuate the respiration capacity of the membrane proteins; and increase the energy generation through the carbohydrate metabolism (Wang et al., 2015). The prior studies have attributed the defense mechanisms of thermophiles to their ability to upkeep protein stability and the enzyme activity under hot conditions (Gerday & Glansdorff, 2007). Based on crystal structure of the reported thermophilic enzymes, the thermostability of the proteins in thermophiles has been attributed to processes related to the amino acid substitutions, hydrophobic cores, buried polar contacts and ion pairs, and interactions among subunits (Wang et al., 2015). A series of genome, transcriptome, and proteome studies, along with the multiple omics information, are required to understand the specific defense mechanisms used by thermophiles in MESs.

3.1.1. The genomic evolution of thermophiles

A shift in the temperature induces genomic evolution, which in turn confers thermal-tolerant abilities under the high temperatures. These evolutionary changes are typically achieved through horizontal gene transfer, gene loss, or gene mutations (Wang et al., 2015).

3.1.2. Base biases of thermophilic genomes

A high guanine and cytosine content contributes to the thermostability of the genome, which is correlated with the growth temperature. A high level of adenine plus guanine content in mRNAs has been identified as a selective response for survival among thermophiles. The base biases affect the variations of amino acid usages and composition in the proteomes of thermophiles. The amino acid usage strategy helps thermophiles adapt to hot conditions (Wang et al., 2015).

3.1.3. Global gene expression responses to high temperatures

Thermophiles elicit a prompt physiological response to temperature changes by forming a functional network within the cells and maintaining the optimal expression status of certain genes (Goh et al., 2017). The transcriptome and proteome data at the opposite sides of central dogma represent the gene expression status in thermophiles. The integration of the two sets of gene expression data constitutes a foundation for investigating the adaptive mechanisms of thermophiles (Wang et al., 2015).

3.1.4. Thermostability of proteins

The pH or salt concentration can vary in the inner cellular boundaries when compared to that in the outer cell boundaries. However, temperature can affect the cells that are not necessarily characterized by differences in the temperatures at the outer and inner cellular boundaries. Most often, the thermophiles grown under high temperatures face a challenge to stabilize their cellular proteins in the native configurations (Gerday & Glansdorff, 2007; Wang et al., 2015). Recent proteomic developments offer a convincing evidence to support stability of proteins in thermophiles (Wang et al., 2015).

Table 3
Ionic Composition of Different Types of Salt Lakes.

	Great Salt Lake	Marine Saltern	Zugm Soda Lake	Gaar Soda Lake	Dead Sea
Na^+	105.4	65.4	142	137	39.2
K^+	6.7	5.2	2.3	1.4	7.3
Mg^{2+}	11.1	20.1	–	–	40.7
Ca^{2+}	0.3	0.2	–	–	16.9
Cl^-	181	144	154.6	173.7	212.4
so_4^{2-}	27	19	22.6	48	0.5
Carbonates	0.7	–	67.2	6.6	0.2
Total salts	332.5	253.9	393.9	374.2	322.6
pH	7.7	7	11	10.9	6

Adapted from (Litchfield, 1998).

Fig. 3 presents an omics perspective about the different adaptation mechanisms used by thermophiles, specifically related to genetic selection and functional acclimatization (Fig. 3) (Wang et al., 2015). The omics data can delineate the following aspects of defense strategies used by thermophiles: the macromolecules that participate in heat shock responses; the molecular machinery for synthesizing thermostable proteins; and the functional network used to acclimatize the proteins under high temperatures.

3.2. Defense mechanisms of halophiles

Table 3 provides an overall ionic composition of hypersaline lakes that are characterized by both the neutral and alkaline lakes. Halophiles have been reported to survive in both the neutral and alkaline types of hypersaline lakes, even when the salt concentration is as high as 15% (w/v).

The first defense mechanism used by the halophiles involves an accumulation of molar concentrations of K^+ and Cl^-. This strategy requires an extensive adaptation of the intracellular enzymatic machinery to the salts, because the indigenous proteins will be required to maintain their conformation and activity under saturated salt conditions. Halophiles adapt by regulating the salt concentration in their cytoplasm. In turn, the cytoplasmic proteins of the halophiles adapt to the environment by accumulating anionic amino acids on the cell surfaces for improving the stability and activity of the proteins in the non-aqueous solvents. Halophiles reduce their osmotic pressure by gathering high levels of low-molecular-weight neutral organic species (Crowley, 2017; Litchfield, 1998). Another strategy is based on the biosynthesis or accumulation of osmolytes (e.g., ectoine and glycine betaine), especially in terms of the biochemical adaptations of their proteins, lipids, and nucleic acids (Litchfield, 1998). These details are summarized below.

3.2.1. Proteins

Halophilic archaeal proteins are modified to contain high levels of acidic amino acids (glutamic acid and aspartic acid). The excess acidic amino acid residues (12–20 mol%) on the external surface of the protein and around the N-termini stabilize the helices through the salt bridge. As the internal concentration of K^+ ions become equivalent to the external concentration of Na^+, the ionic interaction between the negative charges on the proteins and the K^+ ions enable the formation of a hydration shell around the proteins. Further, many enzymes require an elevated levels of K^+ to maintain their activity. Such ionic

Table 4
Performance of select extremophiles in MESs.

MES	Extremophile	pH	Strain	Application	Summary of Parameter			Ref
					Electron donor	Current	CE	
Thermophile								
MFC	> 80 °C	7.40	*Caldanaerobacter subterraneus* *Thermodesulfobacterium commune*	Wastewater treatment at extremely high temperatures	Oil field formation water	350 mA/m^2	–	(Fu et al., 2015)
MEC	60 °C	7.00	*Thermoanaerobacter pseudethanolicus*	Electricity generation from xylose, glucose, cellobiose, and acetate	Xylose	5800 mA/m^2	35	(Lusk et al., 2015)
MEC	60 °C	6.95	*Thermincola ferriacetica*	Determination of maximum rates of anode respiration by *T. ferriacetica*	Acetate	8000 mA/m^2	93	(Parameswaran et al., 2013)
MFC	55 °C	7.0–7.2	*Firmicutes*	Investigation of microbial diversity using ethanol as substrate	Ethanol	2 A/m^2	–	(Dai et al., 2017)
MFC	55 °C	–	*Caloramator australicus*	Investigation of phylogenetic diversity of thermophilic exoelectrogen for industrial application	Anaerobic sludge	1.3 mA	–	(Fu et al., 2013)
MFC	55 °C	6.80	*Thermincola* sp.	Current generation using gram-positive bacteria	Acetate	0.55 mA	89	(Wrighton et al., 2008)
MFC	55 °C	4–7	*Thermoanaerobacter Bacillus*	Understanding metabolic shift in thermophilic MCF	Glucose	–	–	(Zhang et al., 2016)
MFC	60 °C	6.3–6.5	Microbes on marine marsh sediment	Electricity generation from marine sediment	Cellulose or acetate	254 mA/m^2	45	(Mathis et al., 2008)
MFC	60 °C	–	*Thermincola ferriacetica*	Characterization of electrochemical properties of the Gram-positive, thermophilic bacterium	Acetate	400 mA/ m^2	97	(Marshall & May 2009)
MFC	55 °C	7.00	Microbes from anaerobic digester	Electricity generation from artificial wastewater	Acetate	5 mA	96	(Jong et al., 2006)
MFC	55 °C	7.00	*Bacteroidetes*	Removal of sulfate along with oxidation of organic substrates in high temperature wastewater	Distillery wastewater	2.3 A/m^2	89	(Ha et al., 2012)
MFC	60 °C	7.00	*Thermincola ferriacetica*	Application *T. ferriacetica* for waste treatment	Acetate	400 mA/m^2	97	(Marshall & May 2009)
MFC	50 °C	7.00	*Bacillus licheniformis* *Bacillus hermoglucosidasius*	Investigation of effect of carbon sources used in the initial culture medium of thermophilic MFC	Fructose, galactose, glucose, lactose, maltose, mannitol, mannose, sorbitol, starch, sucrose, and trehalose	0.03 mA/m^2	41	(Choi et al., 2004)
Halophile								
MEC	100 g/L NaCl	5.4–7	*Desulfuromonas* *Geoalkalibacter*	Recovery of energy from olive brine wastewater	Olive brine wastewater	7.5 A/m^2	30	(Marone et al., 2016)
MEC	25% Salinity	7–11	*Bacteroides*	Waste treatment at thermophilic and hypersaline conditions	Acetate	6.8 A/m^2	–	(Shehab et al., 2017)
MFC	NA	–	*Exiguobacterium acetylicum*	Electricity generation from reductive decolorization of reactive blue 160	LB media	–	–	(Chen et al., 2013)
MEC	1.7% Salinity	7–9.3	*Geoalkalibacter spp*	Waste treatment under expanded ranges of salinity and pH	Acetate	8.3 A/m^2	95	(Badalamenti et al., 2013)
MXC	45 g/L Salinity	–	*Desulfuromonas soudanensis*	Enrichment of rare metal reducers using electrode-based approaches	Acetate	–	–	(Badalamenti et al., 2016)
MFC	0–20% NaCl	–	*Shewanella marisflavi EP1*	Treatment of textile wastewater	Lactate	–	–	(Xu et al., 2016)
MEC	35 g/L NaCl	7.6–8	*Proteobacteria*	Treatment of saline effluents and continuous production of hydrogen		203 A/m^3	80	(Carmona-Martínez et al., 2015)
MFC	100 g/L NaCl	–	*H. praevalens* *M. hydrocarbonoclasticus*	Desalination and reuse of hypersaline wastewaters.	Produced wastewater	0.42 mA	10	(Monzon et al., 2016)
MFC	100 g/m^3 Salinity	9	*Stenotrophomonas* spp.	Treatment of seafood processing wastewater	Seafood processing effluent	–	28	(Jayashree et al., 2016)
MFC	3.5% NaCl	–	*Geoalkalibacter subterraneus*	Investigation of possible anodic electron transfer mechanisms	Acetate	5 A/m^2	114	(Carmona-Martínez et al., 2013)
MFC	100 g/L NaCl	7.50	*Halanaerobium praevalens*	Treatment of Hydraulic fracturing oil and gas wastewater	Sea sediments	–	–	(Monzon et al., 2017)
MFC	90–346 g/L Salinity	7.00	*Haloferax volcanii* *Natrialba magadii*	Scale up of archaea MFC	Tryptic soy broth	22.03 µA/cm^2	–	(Abrevaya et al., 2011)
MXC	> 200 g/L Salinity	6.57	Facultative anaerobic sludge from desalination plant	Treatment of organic content of produced water	Produced water	2.8 mA/m^3	0.2	(Naraghi et al., 2015)
MFC	45 g/L Salinity	6.5–7.4	Mediterranean sea microorganism	Operation of microbial bioanodes in high conductivity electrolytes	Acetate	85 A/m^2	22.7	(Rousseau et al., 2013)
MFC	> 35 g/L NaCl	7.5–7.8	Great Salt Lake	Wastewater treatment	–	820 mA/m^2	–	(Grattieri et al., 2017

Note: **MES**-Microbial electrochemical system, **MFC**-Microbial fuel cell, **MEC**-Microbial electrolysis cell, **MXC**-Microbial electrochemical cell, **CE**-Coulombic efficiency, **NA**-Not available.

environment and the acidic nature of the proteins involve a series of interactions, resulting in the protein stabilization. This provides a conducive aqueous environment that supports the functionality of the proteins that are found on the exterior cell surfaces or within the intracellular cytoplasmic environments.

3.2.2. Lipids

The halophiles contain a unique set of lipids that are composed of ether linkages to the glycerol. These ether-linked side chains are comprised of four to five branched isoprenoid units. This combination is stable in the ionic environment while maintaining the proper membrane fluidity to allow the passage of molecules across the cell wall membrane complex. These lipids are essential for maintenance of the outer and cytoplasmic membranes as they are less prone to hydrolysis (Litchfield, 1998).

3.2.3. Nucleic acids

Although many bacteria have high guanine to cytosine ratio in their DNA, the guanine plus cytosine content in all of the known halophilic Archaea ranges from 59.5 to 71.2% (Litchfield, 1998; Moore & McCarthy, 1969). The high guanine plus cytosine content allows for an extra H-bonding that increases the stability of the DNA when exposed to the high intracellular cation concentrations.

4. Thermophilic MESs

4.1. Summary of existing studies

Table 4 provides an overview of the MESs operated under thermophilic conditions (55 to 80 °C). Examples of the studied thermophiles include *Thermodesulfobiaceae* sp., (Dai et al., 2017), *Thermoanaerobacter pseudethanolicus* (Lusk et al., 2015), *Caldanaerobacter subterraneus* (Fu et al., 2015), *Thermodesulfobacterium commune* (Fu et al., 2015), *Thermincola ferriacetica* (Marshall & May 2009; Parameswaran et al., 2013), *Caloramator australicus* (Fu et al., 2013), *Thermincola* sp.*,* (Wrighton et al., 2008), *Thermoanaerobacter* sp., (Zhang et al., 2016)*, Bacillus* sp., (Choi et al., 2004; Zhang et al., 2016) and *Bacteroidetes* sp. (Ha et al., 2012). Majority of these studies investigated the effects of the physiological parameters (temperature, pH, and buffer concentrations) on the MES performance. For example, Parameswaran et al., 2013 assessed the effects of the pH on the growth of *T. ferriacetica* biofilms on the electrode surfaces at 60 °C. Their study concluded that *T. ferriacetica* generates lower electric current under acidic conditions when compared with neutral and alkaline conditions. They have also indicated that the thermophiles yields higher current density under higher bicarbonate buffer, indicating that the buffer can alleviate pH depression and enhance the thickness of *T. ferriacetica* biofilms.

Owing to the differences in the MES architectures (e.g., electrode and membrane materials, inter-electrode spacing, and physiological conditions) used by different researchers (Table 4), it is not possible to directly compare their performances. Nevertheless, thermophiles can be expected to yield impressive performance in MESs (e.g., current density of 8 A/m^2 by *Thermincola ferriacetica)* (Parameswaran et al., 2013).

4.2. Electrocatalysis

Bio-electrocatalysis refers to a type of catalysis that influences the rates of bio-electrochemical reactions on an electrode surface. The electrocatalysis rates will be influenced by both the physiological conditions (temperature, pressure, ionic conductivity, and electrode potential) and the physicochemical characteristics of the waste streams (e.g., temperature and total dissolved solids of complex waste streams). The prior studies indicate the electroactive nature of the thermophiles (Table 5). Thermophiles offer performance benefits in the MESs by enabling the MES operations at elevated temperature, enhancing rates of substrate oxidation, providing higher product yield, increasing the range of amenable substrates, and finally enhancing bio-electrocatalysis rates by improving the enzyme induction process (Table 4). The selectivity varies with the type of thermophilic strain and the corresponding enzymes. Nevertheless, a broad specificity is advantageous for MES applications. Thermophile isolates can use cellulose and lignin substrates and they may obviate the need for the co-cultures in MESs. For example, Zhiyong's group have used a defined coculture (cellulolytic fermenter *Clostridium cellulolyticum* and the electrogenic *Geobacter sulfurreducens)* to treat cellulose substrates in MFCs (Ren et al., 2007).

Efforts are underway by our group to develop thermophilic *Geobacillus* sp. strain WSUCF1 for treating complex substrates (e.g., prairie cordgrass and food waste) in MFCs (Shrestha et al., 2017c). This study will facilitate the use of monocultures of thermophiles for treating complex substrates in MFCs (> 60 °C). Bhalla et al. (2013) reported the draft genome sequence of strain WSUCF1 that was originally isolated from the compost facility. The *Geobacillus* sp. strain contains genes encoding glycoside hydrolases that has the potential to degrade lignocellulosic biomass (Bhalla et al., 2013). The genome of strain WSUCF1 contains 865 open reading frames (ORFs) for carbohydrate metabolism, out of which 70 ORFs are involved in polysaccharide degradation, 13 ORFs in xylan degradation, and 3 in cellulose degradation (Bhalla et al., 2015). Thermostable xylanase enzymes produced by the strain WSUCF1 exhibit high thermostability compared to those from other model microorganisms (Bhalla et al., 2015). They exhibit optimal growth rates under temperatures as high as 70 °C under neutral pH conditions. Their half-lives were also found to be as high as 18 and 12 days at 60 and 70 °C, respectively (Bhalla et al., 2015). Thermostable xylanase produced by strain WSUCF1 exhibit enhanced activity and high tolerance to xylose. For example, WSUCF1 incubated with p-nitrophenyl xylopyranoside secretes β-xylosidase enzyme, whose specific activity was as high as 133 U/mg. In a recent study by our group, we have investigated the extracellular electron transfer capabilities of a previously unexplored *Geobacillus* sp. strain WSUCF1 in MFCs (Shrestha et al., 2017b) .

The earlier studies indicate that *Thermincola ferriacetica* strain Z-0001 and *Thermincola* sp. strain JR generates electric current from carbon substrates using the electrode as the sole terminal electron acceptor (Marshall & May 2009; Wrighton et al., 2008). Mixed cultures based on *Thermincola carboxydophila* and others related to *T. carboxydophila*, uncultured Firmicutes and *Deferribacteres* (43 mW/m^2 at 60 °C) were also found to generate electric current in absence of external mediator supplements. These studies indicates the ability of the thermophiles to participate in the direct electron transfer (DET) processes.

A study by Wegener et al. (2015) provides an interesting observation on the direct interspecies electron transfer (DIET) between anaerobic methanotrophic archaea (ANME) and sulfate reducing bacteria (SRB) under thermophilic conditions (60 °C) (Wegener et al., 2015). In the natural environments of marine sediments, the consortia consisting of ANME and SRB have been reported to mediate the anaerobic oxidation of methane. ANME oxidizes methane and transfers the electrons to SRB HotSeep-1, which further mediates sulfate reduction. Under the thermophilic conditions that have been reported to favor anaerobic oxidation of methane, ANME and SRB express extracellular cytochromes that facilitate the cell-cell contact and results in the DIET between them. It has been reported that HotSeep-1 can upregulate genes for pili nanowires in presence of the methane. Finally, these studies conclude that the syntrophic growth of anaerobic methanotrophic consortia is driven by the DIET between ANME-1 and HotSeep-1 (Wegener et al., 2015).

Olloqui-Sariego et al. (2014) have carried out a detailed study to investigate the effects of temperature on the electron-transfer kinetics of thermophilic protein Plastocyanin from *Phormidium laminosum.* These proteins were found to be adsorbed on 1,ω-alkanedithiol self-assembled monolayers (SAMs) deposited on gold (Olloqui-Sariego et al., 2014). The electron transfer rates were studied as a function of

Table 5
Extracellular electron transfer mechanism in halophiles and thermophiles.

BES	Temperature/ Salinity	Inocula	Mechanism	Tool used	Ref
Thermophiles					
MFC	60 °C	*Thermincola potens* strain JR	Direct electron transfer	CV	(Wrighton et al., 2011)
MFC	55 °C	*Thermincola potens* strain JR	Support multiheme c-type cytochromes involvement in conducting electrons across the cell envelope of a gram-positive bacterium	LC-MS/MS experiments and Surface-enhanced Raman spectroscopy	(Carlson et al., 2012)
NA	0–90 °C	*Phormidium laminosum*	Variable amount of electroactive protein depending on chain length of the 1,ω-alkanedithiol self-assembled monolayers	CV and Thermal-induced transition mechanism	(Olloqui-Sariego et al., 2014)
MFC	60 °C	*Thermincola ferriacetica*	Direct electron transfer	CV	(Marshall & May 2009)
NA	60 °C	Thermophilic anaerobic methanotrophic archaea consortia	Direct interspecies electron transfer	Draft genome sequencing	(Wegener et al., 2015)
NA	60, 80 and 90 °C	Bacillus schlegelii	Iron-sulfur clusters in ferredoxins are redox active and act as an active site for electron transfer reactions	Electron paramagnetic resonance spectroscopy	(Aono et al., 1995)
Halophiles					
MFC	3.5% NaCl	*Geoalkalibacter subterraneus*	Direct electron transfer	CV and Chronoamperometry	(Carmona-Martínez et al., 2013)
MEC	1.7% NaCl	*Geoalkalibacter spp*	Direct electron transfer	CV and Chronoamperometry	(Badalamenti et al., 2013)
NA	NA	Sea water	Direct extracellular electron transfer	CV and EIS	(Xu et al., 2010)
MFC	NA	*Exiguobacterium acetylicum*	Redox mediators	CV	(Chen et al., 2013)
MFC	NA	*Proteus hauseri*	Redox mediators	CV	(Chen et al., 2011)

Note: **MES**-Microbial electrochemical system, **MFC**-Microbial fuel cell, **MEC**- Microbial electrolysis cell, **CV**-Cyclic voltammetry, **EIS**- Electrochemical impedance spectroscopy, **NA**- Not available.

electrode–protein distance and solution viscosity over a broad range of temperatures (0–90 °C). For both the thin and thick SAMs, the electron-transfer regime was not influenced by the operating temperature. However, for the 1,11-undecanethiol SAM of intermediate chain length, they observed a kinetic regime changeover from a gated or friction-controlled mechanism at low temperatures (0–30 °C) to a non-adiabatic mechanism when the temperature exceeded 40 °C.

The prior studies have established the electrocatalytic activity of the Gram-positive *Thermincola potens* strain JR (Carlson et al., 2012; Wrighton et al., 2011). These studies reveal that the redox-active components were not released by *T. potens* into the electrolyte; instead, the strain JR mediates the direct electron transfer using the c-type cytochrome and transfers the charges from the membrane of the cell to its surface. However, in contrast, other studies suggest that the thicker cell wall and a glycoprotein S-layer in Gram-positive bacteria weakens their ability to mediate the DET reactions (Wrighton et al., 2011).

Thermophilic conditions may improve the prospects for Gram-positive bacteria in the MES applications. This conclusion is based on the finding related to the thermostability of ferredoxin in *Bacillus schlegelii* sp. (Aono et al., 1995). Ferredoxins are non-heme iron proteins that contain redox-active iron-sulfur clusters, which serve as the active sites and facilitate electron transfer reactions. The redox potential of the ferredoxin depends upon the structure of the cluster and its micro-environment. The activity of *Azotobacter*-type 7Fe ferredoxin from *Bacillus schlegelii* has been found to improve by 10, 20 and 30% when the heat treatment temperature increased to 60, 80 and 90 °C, respectively. The increased activity of the ferredoxin at higher temperatures has been attributed to interconversion of [4Fe-4S] cluster to [3Fe-4S] cluster. Ferredoxin remained stable even after five hours of heat treatment at 60 °C (Aono et al., 1995).

4.3. Knowledge gaps

The selection of thermophiles is not a straightforward process and it depend upon a combination of factors related to physico-chemical characteristics of the waste streams, performance targets (current density, coulombic efficiency, power density), process parameters (conversion efficiency, biomass yield of or product-per-electron,), and physiological constraints (growth requirements) (Koch & Harnisch, 2016). Many of the prior studies indicate that thermophiles facilitate both the DET (Carmona-Martínez et al., 2013; Wrighton et al., 2011) and mediated electron transfer (MET) mechanisms (Abrevaya et al., 2011) in MESs (Table 5). Further studies may be required to discern the following aspects of thermophiles in MESs: (1) the molecular mechanisms that facilitate the DET through membrane-bound proteins and organelles (cytochromes and pili); (2) the cellular or molecular features that enhance electrocatalytic performance; (3) an optimal combination of electrolyte viscosity, inter-electrode spacing, and temperature that provide a suitable protein conformation that promotes electron transfer capabilities of thermophiles. What are the unique electron transfer mechanisms that help thermophiles use recalcitrant substrates as the electron donors, especially under the thermal shock imposed by thermophilic conditions? What are the unique morphological and physiological characteristics that help thermophiles resist temperature shock?

Further studies are required to delineate the relative contributions of operating conditions (i.e., high temperature) and the physiology parameters (e.g., nanowire conductivity) to the enhanced electroactivity of thermophiles. The system level definitions (e.g., coulombic efficiency and current density) for electroactivity do not take into account the influence of the cellular physiology parameters (e.g., nanowire conductivity, size of cellular redox pool or capacitance, and extracellular electron transfer rates coupled with microbial metabolism). Further, owing to the variations in the experimental set up and techniques used in different MES studies, it may not be fair to use the system level parameters for comparing electroactivity of thermophiles with other model organisms. To ascertain the enhanced electroactivity by extremophiles, studies are warranted to quantify the following parameters: cell growth rates; redox reaction kinetics of relevant Faradaic reactions; electron transfer rates; and interplay between the factors related to electroactive bacteria (extracellular transfer mechanisms and associated kinetics), underlying electrode surface (surface properties, electron transfer properties), and physiological conditions (concentration, pH, temperature). Nevertheless, thermophiles provide an exciting opportunity for treating a range of complex substrates in MESs (microbial fuel cells, microbial electrolysis cells, microbial desalination cells, and microbial electro synthesis) under a broad range of harsh conditions including cold, hot, acidic, and alkaline conditions. They can pave a path for developing MESs for the deep biosphere and extraterrestrial applications.

4.4. Unique applications

Thermophiles provide a good platform for treating complex substrates such as marine sediments (Mathis et al., 2008), oil and gas wastewater (Fu et al., 2015), distillery wastewater (Ha et al., 2012), and municipal wastewater (Jong et al., 2006) (Table 4). They can also treat wastewaters from alcohol distilleries, hydrothermal vents, breweries, and meat industry. Thermophiles offer triple benefits: waste treatment, pathogen inhibition, and generation of electricity or valuable products.

4.5. Engineering challenges

From the operations standpoint, the large-scale, thermophilic MES operations (< 100 °C) will require sophisticated equipment such as water-jacketed, water bath, or double walled reactor systems. Further, autoclave systems will be required to sustain MES operations at temperatures above 100 °C. From the materials standpoint, thermophilic operations require electrolyte, electrode, and membrane materials to withstand temperatures ranging from 41 to 122 °C. These conditions pose the following challenges: (1) corrosion and microbial corrosion of the metals; (2) membrane degradation and associated reduction in conductivity (Chandan et al., 2013); and (3) reduced solubility of gases in the electrolyte. Thermophilic conditions may result in the formation of gas bubbles and induce an erroneous measurements of electrochemical signals. Reference electrodes can suffer from stability issues when they undergo rapid hydrolysis under aqueous and hot conditions (Wildgoose et al., 2004). The following sections highlight other potential issues in the MESs and corresponding challenges.

4.5.1. Potential effects of thermophilic conditions on redox-active shuttling compounds

A majority of redox-active, shuttling compounds observed in MESs can be expected to remain stable under the thermophilic systems. The melting points of anthraquinone 2,6-disulfonic acid, cobalt sepulchrate, neutral red, azure A, and humic acids lie in a range of 200 to 300 °C. The values of the melting points are an order of magnitude lower when compared with the typical temperatures encountered in the thermophilic MESs (Supplementary Table S2). On the other hand, thermophilic conditions can promote the kinetics of MET reactions facilitated by these shuttling compounds (Table 2).

4.5.2. Frequent media replacements in the thermophilic, fed-batch MESs

Higher temperatures enable faster reaction kinetics and they can demand frequent electrolyte replacement in the fed-batch MESs. This problem can be mitigated by initiating the fed-batch reactor operations with higher substrate loading (i.e., higher substrate). However, this has to be done carefully to prevent any possible adverse effects. For example, in a fed-batch MFC study by Pannell et al. (2016), it was concluded that an increase in the substrate concentration from 1.3 g/L to 2.6 g/L resulted in an enhanced current density; however, a further increase has been reported to be detrimental to the overall performance of the MFCs (Pannell et al., 2016). It is also critical to adopt the field experience from contemporary biological systems (e.g. anaerobic digestions) which have successfully operated in the fed-batch mode to repeat the following benefits: enhanced substrate utilization, enhanced cell growth rates, and higher organic loading rates.

4.5.3. Degradation of proton exchange membranes under high temperatures

Higher temperatures reduce the permeability of the proton exchange membrane (PEM) separators by dehydrating their sulphonated polymer groups. These challenges can be addressed by using the PEM materials (sulfonated hydrocarbon polymers, composite membranes (e.g., polymers doped with graphene oxide), and solid acid membranes) that withstand the hot conditions (Park et al., 2011). The PEMs functionalized with organic and inorganic blocks have also been reported to withstand thermophilic conditions. Examples include phosphoric acid-doped polybenzimidazole membrane; high molecular weight polymer membranes (e.g., N-substituted structures) (Li et al., 2009); sulfonated poly (ether ketone) membranes (Parnian et al., 2017); styrene grafted polyethylene membranes (Nasef et al., 2017); and phosphorylated graphene oxide-sulphonated polyimide composites (Shukla et al., 2016). These membranes remain stable in a temperature range of 60 °C to 160 °C (Nasef et al., 2017; Shukla et al., 2016). The following membranes that have already been explored in the MFC applications: sulfonated polyethersulfone (Zinadini et al., 2017), PEMs based on polybenzimidazole (Angioni et al., 2017); and silica-based organically-functionalized mesostructured fillers (Angioni et al., 2016).

5. Halophilic MESs

5.1. Summary of existing studies

Table 4 provides an overview of the halophiles used in the MES applications. They have been evaluated with the salt concentrations in the electrolytes ranging from 35 to 280 g/L. The evaluated halophiles include *Bacteroides* sp., (Shehab et al., 2017), *Exiguobacterium acetylicum* (Chen et al., 2013), *Geoalkalibacter subterraneus* DSM 23483 (Badalamenti et al., 2013), *Proteobacteria* (Carmona-Martínez et al., 2015), *Geoalkalibacter subterraneus* (Carmona-Martínez et al., 2013), *Halanaerobium praevalens* (Monzon et al., 2016), *M. hydrocarbonoclasticus* (Monzon et al., 2016), *Stenotrophomonas* sp., RB1B (Jayashree et al., 2016), *Halanaerobium praevalens* (Monzon et al., 2017), *Haloferax volcanii* (Naraghi et al., 2015), *Natrialba magadii* (Naraghi et al., 2015), *Desulfuromonas* (Marone et al., 2016) and *Geoalkalibacter* (Marone et al., 2016).

5.2. Electrocatalysis

Halophiles enable MES operations under high pH, elevated levels of dissolved solids, and salinity. The saline conditions are known to minimize unintended consequences of contamination during treatment of unprocessed waste. Higher salinity offers the following additional benefits: enhanced proton transfer across the ion exchange membranes, decreased internal resistance, enhanced current density, and a flexibility to treat a wide array of carbon substrates (Lefebvre et al., 2012). The prior studies have demonstrated the electroactive nature of the in the MESs (Table 5). However, there are limited number of studies that provide in-depth details on the biological mechanisms used by the halophiles in MESs. Following sections provide a generic information about halophiles, and this knowledge can provide a preliminary insight on how halophiles may survive hypersaline environments in MESs.

Genetically edited halophiles have been used to produce a range of products including hydrolases amylases, xylanases and cellulases, proteases, β-Carotene, and glycerol (Yin et al., 2015). Unlike typical proteins that undergo aggregation, denaturation, and precipitation under saline conditions, proteins expressed by the halophiles remain stable under the elevated levels of salinity. Genomic and structural analyses have established that the enzymes of halophilic Archaea and bacteria are negatively charged due to excessive acidic residues, which enhance their solubility, and promote their function under low water activity conditions.

The members of halophilic Archaea group prefer aerobic or facultative anaerobic conditions (oxygen or nitrate as the terminal electron acceptor), conferring them an ability to metabolize carbon substrates under a range of reducing conditions (Litchfield, 1998). Pure cultures of obligate anaerobic haloarchaea (e.g. halobacteriaceae) have been reported to grow exclusively by the sulfur respiration (Sorokin et al., 2016). Anaerobic halotolerant bacteria (e.g. *Mobilitalea sibirica*) hydrolyze complex polymeric substrates such as peptone, xylose, trehalose, maltose, cellobiose, dextrin, xanthan gum, lichenan, xylan, filter paper, CM-cellulose and microcrystalline cellulose (Podosokorskaya et al., 2014).

It has been reported in several studies that cytochrome represent a major component of the respiratory chain used by the halophiles (Cheah, 1970a; Cheah, 1970c). A classic study by Cheah's group has provided a first insight on the presence of cytochromes a3 and o in *Halobacterium cutirubrum* and *Halobacterium salinarium* (Cheah, 1970a; Cheah, 1970c). Archaebacterium and *Halobacterium halobium* contains b-type cytochromes and a low levels of cytochromes *o* and a_1 (Cheah, 1970b; Gradin & Colmsjö, 1989). Electron transport chain in *Halobacterium cutirubrum* was characterized by a-type, b-type, and c-type cytochromes (Lanyi, 1968). An aerobic haloalkaliphilic archaebacterium (*Natronobacterium pharaonic*) has been reported to express a high level of redox proteins, cytochrome bc, cytochrome *c*, cytochrome ba_3, and ferredoxin under halophilic conditions (Scharf et al., 1997). A recent study has demonstrated that the tricarboxylic acid cycle of *Desulfuromonas soudanensis* strain contains 38 putative multi-heme c-type cytochromes, along with a cytochrome predicted to lie within a putative prophage (Badalamenti et al., 2016). However, further studies are required to establish the specific roles of these cytochromes on the extracellular electron transfer capabilities of the halophiles in MESs.

A recent study showed that *Desulfuromonas soudanensis* releases electrons at positive potentials (100 mV higher than the typical potentials) compared to *Geobacter sulfurreducens* (Badalamenti et al., 2016). This study suggest that extracellular respiration of *D. soudanensis* is tuned for higher potential electron acceptors (Badalamenti et al., 2016). Halotolerant strain *Shewanella marisflavi* EP1 has been used to decolorize the azo dyes (Xu et al., 2016). *Lactococcus lactis* and *P. hauseri* have also been used for the reductive decolorization of reactive blue 160 (Chen et al., 2013; Chen et al., 2011). However, it is uncertain if these halophiles exhibit electrogenic capabilities. The electric current observed in these strains could be due to the presence of redox-active species (riboflavin and flavin-type compounds) in their culture media.

5.3. Knowledge gaps

Table 5 provides a summary of the studies that investigated the modes of extracellular electron transfer (EET) mechanisms in halophiles. These studies indicate that EET in halophiles is either based on the DET or MET mechanisms. However, their findings are primarily based on the electroanalytical analysis and they do not necessarily identify the underpinning biological mechanism responsible for the EET processes. Modern sequencing techniques (whole genome sequencing) can be combined with classic electrochemical tools (cyclic voltammetry) to discern the electron transfer mechanisms in halophiles. Although electron transfers mechanisms have been well established in electrogens from *Geobacteraceae* and *Shewanaellaceae* families, such comprehensive studies are yet to be established for the recently reported halophiles. Specifically, it is important to establish the ecology and growth characteristics of the halophiles in MESs, under the combined influence of salinity, pH, and temperature. Studies are also warranted to evaluate the use of unexplored haloalkalithermophiles, haloalkaliphiles, and halothermophiles in MESs.

5.4. Unique applications

The earlier studies have used halophiles for treating brine waste, seafood processing effluent, produced water, and sea sediments. Saline wastewater reduce ohmic losses and enhance electrical performance of MESs (Carmona-Martínez et al., 2013; Rousseau et al., 2013). Our recent studies demonstrate the use of halophile-based MESs for treating produced water generated during crude oil production from the fractured Bakken shale. The produced water is characterized by extremely high levels of total dissolved solids (150 g/L), chemical oxygen demand (10 g/L), toxic and radioactive elements, and a range of xenobiotic compounds (Shrestha et al., 2017a). 94% of microbial population in the biofilm conditioned in saline media was based on *Chromohalobacter* sp. We evaluated the feasibility of treating the produced water in both the MFCs and MCDCs. The polarization resistance (6600 $\Omega.cm^2$) in the MCDCs was one order of magnitude higher when compared to the MFCs (870 $\Omega.cm^2$). However, the MCDCs achieved two-fold higher total dissolved solids removal when compared to that in the MFCs (Shrestha, 2017).

Halophiles provide a new platform for treating saline wastewaters from agriculture, aquaculture, and industrial sectors. The seawater, brines and industrial wastewater represent an untapped sources of critical metals and elements. The halophiles in MESs can likely be used to mine critical metals and elements from brine wastes. They can also be used to harvest valuable chemicals from the saline waste streams.

5.5. Engineering challenges

Hyper-saline environments pose a series of material degradation challenges (biofouling and corrosion) to the exposed electrode and membrane materials in MESs. Electrodes, current collectors, and fittings based on the metals that are exposed to higher levels of chloride ions are susceptible to pitting or galvanic corrosion. The material degradation issues will eventually appear in the form of measurement anomalies, increased impedance, and reduced performance of MESs. Corrosion resistant material will address some of these issues but they are expensive compared to conventional materials (Oren, 2010). Aromatic polyether ether ketone (PEEK) polymers and borosilicate materials are the two possible materials that withstand hypersaline environments (Lorantfy et al., 2014).

MESs based on aerobic halophiles will face challenges posed by the low oxygen solubility under saline conditions. This challenge can be addressed by using a gas distribution device with nozzles to pump smaller quantities of air to enhance the concentration of dissolved oxygen (Hezayen et al., 2000). Saline electrolytes can induce the fouling issues due to alkalization, evaporation, sorption, and crystallization processes (Jiang et al., 2011; Zhuang et al., 2012). PEMs exposed to high salinity will suffer from fouling problems due to concentration polarization. In our recent study, we indicated that the electrode and membrane materials exposed to the produced water from the Bakken shale are gradually fouled with the crystalline deposits of salt, and the fouling issues became apparent within 80 days of the MCDC operation (Shrestha, 2017; Shrestha et al., 2018). The electrochemical impedance spectroscopy analysis showed that the fouling issues result in a gradual increase in the overall impedance of both the MFCs and MCDCs that are fed with the produced water (Shrestha, 2017; Shrestha et al., 2018). Other recent studies have also corroborated that the electrolytes based on the brackish water can foul the electrode and membrane materials in MESs (Jiang et al., 2011; Zhuang et al., 2012).

6. Conclusion

Microbial electrochemical systems exhibit an unlimited potential to change our lives in many exciting ways. Their performance can be fully optimized by performing bio-electrochemical reactions at extremes of temperature and salinity. However, further studies are required to uncover the secrets behind the enhanced electrocatalytic activity of the extremophiles. It is currently unknown if the unique cellular and morphological characteristics of extremophiles promote their electrocatalytic activity. It is also unknown if they live under the harsh conditions by a chance or due to a necessity. Nevertheless, extremophiles present new opportunities for transforming recalcitrant waste streams into valuable products.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biortech.2018.01.151.

References

Abrevaya, X.C., Sacco, N., Mauas, P.J., Cortón, E., 2011. Archaea-based microbial fuel cell operating at high ionic strength conditions. Extremophiles 15 (6), 633.

Alkhalili, R.N., Hatti-Kaul, R., Canbäck, B., 2015. Genome sequence of Geobacillus sp. strain ZGt-1, an antibacterial peptide-producing bacterium from hot springs in Jordan. Genome Announc. 3 (4), e00799–15.

Angioni, S., Millia, L., Bruni, G., Tealdi, C., Mustarelli, P., Quartarone, E., 2016. Improving the performances of Nafion™-based membranes for microbial fuel cells with silica-based, organically-functionalized mesostructured fillers. J. Power Sources 334, 120–127.

Angioni, S., Millia, L., Bruni, G., Ravelli, D., Mustarelli, P., Quartarone, E., 2017. Novel composite polybenzimidazole-based proton exchange membranes as efficient and sustainable separators for microbial fuel cells. J. Power Sources 348, 57–65.

Aono, S., Fukuda, N., Okura, I., 1995. Thermostability and electron transfer activity of the ferredoxin from a thermophilic hydrogen oxidizing bacterium, Bacillus schlegelii. J. Mol. Catal. A: Chem. 95 (2), 173–178.

Babu, P., Chandel, A.K., Singh, O.V., 2015. Survival Mechanisms of Extremophiles. In: Extremophiles and Their Applications in Medical Processes. Springer, pp. 9–23.

Badalamenti, J.P., Krajmalnik-Brown, R., Torres, C.I., 2013. Generation of high current densities by pure cultures of anode-respiring Geoalkalibacter spp. under alkaline and saline conditions in microbial electrochemical cells. MBio 4 (3), e00144–13.

Badalamenti, J.P., Summers, Z.M., Chan, C.H., Gralnick, J.A., Bond, D.R., 2016. Isolation and genomic characterization of 'Desulfuromonas soudanensis WTL', a metal-and electrode-respiring bacterium from anoxic deep subsurface brine. Front. Microbiol. 7.

Baliga, N.S., Bonneau, R., Facciotti, M.T., Pan, M., Glusman, G., Deutsch, E.W., Shannon, P., Chiu, Y., Weng, R.S., Gan, R.R., 2004. Genome sequence of Haloarcula marismortui: a halophilic archaeon from the Dead Sea. Genome Res. 14 (11), 2221–2234.

Barnard, D., Casanueva, A., Tuffin, M., Cowan, D., 2010. Extremophiles in biofuel synthesis. Environ. Technol. 31 (8–9), 871–888.

Bezuidt, O.K., Makhalanyane, T.P., Gomri, M.A., Kharroub, K., Cowan, D.A., 2015. Draft genome sequence of thermophilic Geobacillus sp. strain Sah69, isolated from Saharan soil, southeast Algeria. Genome Announce. 3 (6), e01447–15.

Bhalla, A., Kainth, A.S., Sani, R.K., 2013. Draft genome sequence of lignocellulose-degrading thermophilic bacterium Geobacillus sp. strain WSUCF1. Genome Announce. 1 (4), e00595–13.

Bhalla, A., Bischoff, K.M., Sani, R.K., 2015. Highly thermostable xylanase production from a thermophilic Geobacillus sp. strain WsUcF1 utilizing lignocellulosic biomass. Front. Bioeng. Biotechnol. 3.

Burgess, S.A., Cox, M.P., Flint, S.H., Lindsay, D., Biggs, P.J., 2015. Draft genome sequences of three strains of Geobacillus stearothermophilus isolated from a milk powder manufacturing plant. Genome Announce. 3 (5), e00939–15.

Carlson, H.K., Iavarone, A.T., Gorur, A., Yeo, B.S., Tran, R., Melnyk, R.A., Mathies, R.A., Auer, M., Coates, J.D., 2012. Surface multiheme c-type cytochromes from Thermincola potens and implications for respiratory metal reduction by Gram-positive bacteria. Proc. Natl. Acad. Sci. 109 (5), 1702–1707.

Carmona-Martínez, A.A., Pierra, M., Trably, E., Bernet, N., 2013. High current density via direct electron transfer by the halophilic anode respiring bacterium Geoalkalibacter subterraneus. Phys. Chem. Chem. Phys. 15 (45), 19699–19707.

Carmona-Martínez, A.A., Trably, E., Milferstedt, K., Lacroix, R., Etcheverry, L., Bernet, N., 2015. Long-term continuous production of H 2 in a microbial electrolysis cell (MEC) treating saline wastewater. Water Res. 81, 149–156.

Challacombe, J.F., Majid, S., Deole, R., Brettin, T.S., Bruce, D., Delano, S.F., Detter, J.C., Gleasner, C.D., Han, C.S., Misra, M., 2013. Complete genome sequence of Halorhodospira halophila SL1. Standards Genom. Sci. 8 (2), 206.

Chan, M., Himes, R.H., Akagi, J., 1971. Fatty acid composition of thermophilic, mesophilic, and psychrophilic clostridia. J. Bacteriol. 106 (3), 876–881.

Chandan, A., Hattenberger, M., El-Kharouf, A., Du, S., Dhir, A., Self, V., Pollet, B.G., Ingram, A., Bujalski, W., 2013. High temperature (HT) polymer electrolyte membrane fuel cells (PEMFC)–a review. Journal of Power Sources. 231, 264–278.

Cheah, K., 1970a. Effect of K+ and Na+ on the cytochrome oxidase activity of Halobacterium cutirubrum. FEBS Lett. 7 (3), 301–303.

Cheah, K., 1970b. The membrane-bound ascorbate oxidase system of Halobacterium halobium. Biochim. Biophys. Acta (BBA)-Bioenergetics 205 (2), 148–160.

Cheah, K., 1970c. Properties of the membrane-bound respiratory chain system of Halobacterium salinarium. Biochim. Biophys. Acta (BBA)-Bioenergetics 216 (1), 43–53.

Chen, B.-Y., Wang, Y.-M., Ng, I.-S., 2011. Understanding interactive characteristics of bioelectricity generation and reductive decolorization using Proteus hauseri. Bioresour. Technol. 102 (2), 1159–1165.

Chen, B.-Y., Hong, J., Ng, I.-S., Wang, Y.-M., Liu, S.-Q., Lin, B., Ni, C., 2013. Deciphering simultaneous bioelectricity generation and reductive decolorization using mixed-culture microbial fuel cells in salty media. J. Taiwan Inst. Chem. Eng. 44 (3), 446–453.

Choi, Y., Jung, E., Park, H., Paik, S.R., Jung, S., Kim, S., 2004. Construction of microbial fuel cells using thermophilic microorganisms, Bacillus licheniformis and Bacillus thermoglucosidasius. Bull.-Korean Chem. Soc. 25 (6), 813–818.

Copeland, A., O'Connor, K., Lucas, S., Lapidus, A., Berry, K.W., Detter, J.C., Del Rio, T.G., Hammon, N., Dalin, E., Tice, H., 2011. Complete genome sequence of the halophilic and highly halotolerant Chromohalobacter salexigens type strain (1H11 T). Standards Genom. Sci. 5 (3), 379.

Crowley, E., 2017. Compatible solute ectoine review: protection mechanisms and production methods. J. Undergraduate Stud. Trent (JUST). 5 (1), 32–39.

Dai, K., Wen, J.-L., Zhang, F., Ma, X.-W., Cui, X.-Y., Zhang, Q., Zhao, T.-J., Zeng, R.J., 2017. Electricity production and microbial characterization of thermophilic microbial fuel cells. Bioresour. Technol. 243, 512–519.

DasSarma, S., DasSarma, P., 2015. Halophiles and their enzymes: negativity put to good use. Curr. Opin. Microbiol. 25, 120–126.

de-Bashan, L.E., Trejo, A., Huss, V.A., Hernandez, J.-P., Bashan, Y., 2008. Chlorella sorokiniana UTEX 2805, a heat and intense, sunlight-tolerant microalga with potential for removing ammonium from wastewater. Bioresour. Technol. 99 (11), 4980–4989.

De Maayer, P., Williamson, C.E., Vennard, C.T., Danson, M.J., Cowan, D.A., 2014. Draft genome sequences of Geobacillus sp. strains CAMR5420 and CAMR12739. Genome Announce. 2 (3), e00567–14.

Dopson, M., Ni, G., Sleutels, T.H., 2016. Possibilities for extremophilic microorganisms in microbial electrochemical systems. FEMS Microbiol. Rev. 40 (2), 164–181.

ElMekawy, A., Hegab, H.M., Vanbroekhoven, K., Pant, D., 2014. Techno-productive potential of photosynthetic microbial fuel cells through different configurations. Renew. Sust. Energy Rev. 39, 617–627.

Fu, Q., Kobayashi, H., Kawaguchi, H., Vilcaez, J., Wakayama, T., Maeda, H., Sato, K., 2013. Electrochemical and phylogenetic analyses of current-generating microorganisms in a thermophilic microbial fuel cell. J. Biosci. Bioeng. 115 (3), 268–271.

Fu, Q., Fukushima, N., Maeda, H., Sato, K., Kobayashi, H., 2015. Bioelectrochemical analysis of a hyperthermophilic microbial fuel cell generating electricity at temperatures above 80 C. Biosci. Biotechnol. Biochem. 79 (7), 1200–1206.

Gajda, I., Greenman, J., Melhuish, C., Ieropoulos, I., 2013. Photosynthetic cathodes for microbial fuel cells. Int. J. Hydrogen Energy 38 (26), 11559–11564.

Gerday, C., Glansdorff, N., 2007. Physiology and Biochemistry of Extremophiles. American Society of Microbiology.

Goh, K.M., Chan, K.-G., Sani, R.K., Donati, E.R., Reysenbach, A.-L., 2017. Genetics, genomics and omics of thermophiles. Front. Microbiol 8.

Gonzalez, O., Gronau, S., Pfeiffer, F., Mendoza, E., Zimmer, R., Oesterhelt, D., 2009. Systems analysis of bioenergetics and growth of the extreme halophile Halobacterium salinarum. PLoS Comput. Biol. 5 (4), e1000332.

Goo, Y.A., Roach, J., Glusman, G., Baliga, N.S., Deutsch, K., Pan, M., Kennedy, S., DasSarma, S., Ng, W.V., Hood, L., 2004. Low-pass sequencing for microbial comparative genomics. BMC Genom. 5 (1), 3.

Gradin, C.H., Colmsjö, A., 1989. Four different b-type cytochromes in the halophilic archaebacterium, Halobacterium halobium. Arch. Biochem. Biophys. 272 (1), 130–136.

Grattieri, M., Suvira, M., Hasan, K., Minteer, S.D., 2017. Halotolerant extremophile bacteria from the Great Salt Lake for recycling pollutants in microbial fuel cells. J. Power Sources 356, 310–318.

Gude, V., Kokabian, B., Gadhamshetty, V., 2013. Beneficial bioelectrochemical systems for energy, water, and biomass production. J. Microb. Biochem. Technol. 6, 2.

Ha, P.T., Lee, T.K., Rittmann, B.E., Park, J., Chang, I.S., 2012. Treatment of alcohol distillery wastewater using a Bacteroidetes-dominant thermophilic microbial fuel cell. Environ. Sci. Technol. 46 (5), 3022–3030.

Harnisch, F., Schröder, U., 2010. From MFC to MXC: chemical and biological cathodes and their potential for microbial bioelectrochemical systems. Chem. Soc. Rev. 39 (11), 4433–4448.

Hezayen, F., Rehm, B., Eberhardt, R., Steinbüchel, A., 2000. Polymer production by two newly isolated extremely halophilic archaea: application of a novel corrosion-resistant bioreactor. Appl. Microbiol. Biotechnol. 54 (3), 319–325.

Jayashree, C., Tamilarasan, K., Rajkumar, M., Arulazhagan, P., Yogalakshmi, K., Srikanth, M., Banu, J.R., 2016. Treatment of seafood processing wastewater using upflow microbial fuel cell for power generation and identification of bacterial community in anodic biofilm. J. Environ. Manage. 180, 351–358.

Jeong, H., Yim, J.H., Lee, C., Choi, S.-H., Park, Y.K., Yoon, S.H., Hur, C.-G., Kang, H.-Y., Kim, D., Lee, H.H., 2005. Genomic blueprint of Hahella chejuensis, a marine microbe producing an algicidal agent. Nucl. Acids Res. 33 (22), 7066–7073.

Jiang, D., Curtis, M., Troop, E., Scheible, K., McGrath, J., Hu, B., Suib, S., Raymond, D., Li, B., 2011. A pilot-scale study on utilizing multi-anode/cathode microbial fuel cells

(MAC MFCs) to enhance the power production in wastewater treatment. Int. J. Hydrogen Energy 36 (1), 876–884.

Jong, B.C., Kim, B.H., Chang, I.S., Liew, P.W.Y., Choo, Y.F., Kang, G.S., 2006. Enrichment, performance, and microbial diversity of a thermophilic mediatorless microbial fuel cell. Environ. Sci. Technol. 40 (20), 6449–6454.

Koch, C., Harnisch, F., 2016. What is the essence of microbial electroactivity? Front. Microbiol. 7.

Koga, Y., 2012. Thermal adaptation of the archaeal and bacterial lipid membranes. Archaea 2012.

Lanyi, J., 1968. Studies of the electron transport chain of extremelv halophilic bacteria: I. Spectrophotometric identification of the cytochromes of Halobacterium cutirubrum. Arch. Biochem. Biophys. 128 (3), 716–724.

Lefebvre, O., Tan, Z., Kharkwal, S., Ng, H.Y., 2012. Effect of increasing anodic NaCl concentration on microbial fuel cell performance. Bioresour. Technol. 112, 336–340.

Li, Q., Jensen, J.O., Savinell, R.F., Bjerrum, N.J., 2009. High temperature proton exchange membranes based on polybenzimidazoles for fuel cells. Progr. Polym. Sci. 34 (5), 449–477.

Litchfield, C.D., 1998. Survival strategies for microorganisms in hypersaline environments and their relevance to life on early Mars. Meteoritics Planetary Sci. 33 (4), 813–819.

Logan, B.E., 2010. Scaling up microbial fuel cells and other bioelectrochemical systems. Appl. Microbiol. Biotechnol. 85 (6), 1665–1671.

Logan, B.E., Rabaey, K., 2012. Conversion of wastes into bioelectricity and chemicals by using microbial electrochemical technologies. Science 337 (6095), 686–690.

Lorantfy, B., Seyer, B., Herwig, C., 2014. Stoichiometric and kinetic analysis of extreme halophilic Archaea on various substrates in a corrosion resistant bioreactor. New Biotechnol. 31 (1), 80–89.

Lusk, B.G., Khan, Q.F., Parameswaran, P., Hameed, A., Ali, N., Rittmann, B.E., Torres, C.I., 2015. Characterization of electrical current-generation capabilities from thermophilic bacterium Thermoanaerobacter pseudethanolicus using xylose, glucose, cellobiose, or acetate with fixed anode potentials. Environ. Sci Technol. 49 (24), 14725–14731.

Malfatti, S., Tindall, B.J., Schneider, S., Fähnrich, R., Lapidus, A., LaButtii, K., Copeland, A., Del Rio, T.G., Nolan, M., Chen, F., 2009. Complete genome sequence of Halogeometricum borinquense type strain (PR3 T). Standards Genomic Sci. 1 (2), 150.

Marone, A., Carmona-Martínez, A., Sire, Y., Meudec, E., Steyer, J., Bernet, N., Trably, E., 2016. Bioelectrochemical treatment of table olive brine processing wastewater for biogas production and phenolic compounds removal. Water Res. 100, 316–325.

Marshall, C.W., May, H.D., 2009. Electrochemical evidence of direct electrode reduction by a thermophilic Gram-positive bacterium, Thermincola ferriacetica. Energy Environ. Sci. 2 (6), 699–705.

Mathis, B., Marshall, C., Milliken, C., Makkar, R., Creager, S., May, H., 2008. Electricity generation by thermophilic microorganisms from marine sediment. Appl. Microbiol. Biotechnol. 78 (1), 147–155.

Meruelo, A.D., Han, S.K., Kim, S., Bowie, J.U., 2012. Structural differences between thermophilic and mesophilic membrane proteins. Protein Sci. 21 (11), 1746–1753.

Monzon, O., Yang, Y., Li, Q., Alvarez, P.J., 2016. Quorum sensing autoinducers enhance biofilm formation and power production in a hypersaline microbial fuel cell. Biochem. Eng. J. 109, 222–227.

Monzon, O., Yang, Y., Kim, J., Heldenbrand, A., Li, Q., Alvarez, P.J., 2017. Microbial fuel cell fed by Barnett Shale produced water: power production by hypersaline autochthonous bacteria and coupling to a desalination unit. Biochem. Eng. J. 117, 87–91.

Moore, R.L., McCarthy, B.J., 1969. Characterization of the deoxyribonucleic acid of various strains of halophilic bacteria. J. Bacteriol. 99 (1), 248–254.

Morita, M., Watanabe, Y., Saiki, H., 2000. High photosynthetic productivity of green microalga Chlorella sorokiniana. Appl. Biochem. Biotechnol. 87 (3), 203–218.

Naraghi, Z.G., Yaghmaei, S., Mardanpour, M.M., Hasany, M., 2015. Produced water treatment with simultaneous bioenergy production using novel bioelectrochemical systems. Electrochim. Acta 180, 535–544.

Nasef, M., Saidi, H., Yahaya, A., 2017. Radiation-induced grafting of styrene onto polyethylene films for preparation of cation exchange membranes: effect of crosslinking +. Appl. Membr. Sci. Technol. 2 (1).

Olloqui-Sariego, J.L., Moreno-Beltrán, B., Díaz-Quintana, A., De la Rosa, M.A., Calvente, J.J., Andreu, R., 2014. Temperature-driven changeover in the electron-transfer mechanism of a thermophilic plastocyanin. J. Phys. Chem. Lett. 5 (5), 910–914.

Oren, A., Larimer, F., Richardson, P., Lapidus, A., Csonka, L.N., 2005. How to be moderately halophilic with broad salt tolerance: clues from the genome of Chromohalobacter salexigens. Extremophiles 9 (4), 275–279.

Oren, A., 2010. Industrial and environmental applications of halophilic microorganisms. Environ. Technol. 31 (8–9), 825–834.

Ortiz, E.M., Berretta, M.F., Navas, L.E., Benintende, G.B., Amadio, A.F., Zandomeni, R.O., 2015. Draft genome sequence of Geobacillus sp. isolate T6, a thermophilic bacterium collected from a thermal spring in Argentina. Genome Announce. 3 (4), e00743–15.

Pan, Y.-Y., Wang, S.-T., Chuang, L.-T., Chang, Y.-W., Chen, C.-N.N., 2011. Isolation of thermo-tolerant and high lipid content green microalgae: oil accumulation is predominantly controlled by photosystem efficiency during stress treatments in Desmodesmus. Bioresour. Technol. 102 (22), 10510–10517.

Pannell, T.C., Goud, R.K., Schell, D.J., Borole, A.P., 2016. Effect of fed-batch vs. continuous mode of operation on microbial fuel cell performance treating biorefinery wastewater. Biochem. Eng. J. 116, 85–94.

Pant, D., Van Bogaert, G., Diels, L., Vanbroekhoven, K., 2010. A review of the substrates used in microbial fuel cells (MFCs) for sustainable energy production. Bioresour. Technol. 101 (6), 1533–1543.

Pant, D., Singh, A., Van Bogaert, G., Gallego, Y.A., Diels, L., Vanbroekhoven, K., 2011. An introduction to the life cycle assessment (LCA) of bioelectrochemical systems (BES) for sustainable energy and product generation: relevance and key aspects. Renew. Sust. Energy Rev. 15 (2), 1305–1313.

Parameswaran, P., Bry, T., Popat, S.C., Lusk, B.G., Rittmann, B.E., Torres, C.I., 2013. Kinetic, electrochemical, and microscopic characterization of the thermophilic, anode-respiring bacterium Thermincola ferriacetica. Environ. Sci. Technol. 47 (9), 4934–4940.

Park, C.H., Lee, C.H., Guiver, M.D., Lee, Y.M., 2011. Sulfonated hydrocarbon membranes for medium-temperature and low-humidity proton exchange membrane fuel cells (PEMFCs). Progr. Polym. Sci. 36 (11), 1443–1498.

Parnian, M.J., Gashoul, F., Rowshanzamir, S., 2017. Studies on the SPEEK membrane with low degree of sulfonation as a stable proton exchange membrane for fuel cell applications. Iran. J. Hydrogen Fuel Cell 3 (3), 221–232.

Petkauskaite, R., Blom, J., Goesmann, A., Kuisiene, N., 2017. Draft genome sequence of pectic polysaccharide-degrading moderate thermophilic bacterium Geobacillus thermodenitrificans DSM 101594. Braz. J. Microbiol. 48 (1), 7–8.

Pikuta, E.V., Hoover, R.B., 2004. Potential application of anaerobic extremophiles for hydrogen production. Proc. SPIE 203–214.

Podosokorskaya, O., Bonch-Osmolovskaya, E., Beskorovaynyy, A., Toshchakov, S., Kolganova, T., Kublanov, I., 2014. Mobilitalea sibirica gen. nov., sp. nov., a halotolerant polysaccharide-degrading bacterium. Int. J. Syst. Evolut. Microbiol. 64 (8), 2657–2661.

Pore, S.D., Arora, P., Dhakephalkar, P.K., 2014. Draft genome sequence of Geobacillus sp. strain FW23, isolated from a formation water sample. Genome Announce. 2 (3), e00352–14.

Quinn, P., Brain, A., Stewart, L., Kates, M., 1986. The structure of membrane lipids of the extreme halophile, Halobacterium cutirubrum, in aqueous systems studied by freeze-fracture. Biochim. Biophys. Acta (BBA)-Biomembranes 863 (2), 213–223.

Rastogi, G., Muppidi, G.L., Gurram, R.N., Adhikari, A., Bischoff, K.M., Hughes, S.R., Apel, W.A., Bang, S.S., Dixon, D.J., Sani, R.K., 2009. Isolation and characterization of cellulose-degrading bacteria from the deep subsurface of the Homestake gold mine, Lead, South Dakota, USA. J. Ind. Microbiol. Biotechnol. 36 (4), 585.

Rastogi, G., Osman, S., Kukkadapu, R., Engelhard, M., Vaishampayan, P.A., Andersen, G.L., Sani, R.K., 2010. Microbial and mineralogical characterizations of soils collected from the deep biosphere of the former Homestake gold mine, South Dakota. Microb. Ecol. 60 (3), 539–550.

Reed, C.J., Lewis, H., Trejo, E., Winston, V., Evilia, C., 2013. Protein adaptations in archaeal extremophiles. Archaea 2013.

Ren, Z., Ward, T.E., Regan, J.M., 2007. Electricity production from cellulose in a microbial fuel cell using a defined binary culture. Environ. Sci. Technol. 41 (13), 4781–4786.

Rosenbaum, M., He, Z., Angenent, L.T., 2010. Light energy to bioelectricity: photosynthetic microbial fuel cells. Curr. Opin. Biotechnol. 21 (3), 259–264.

Rothschild, L.J., Mancinelli, R.L., 2001. Life in extreme environments. Nature 409 (6823), 1092.

Rousseau, R., Dominguez-Benetton, X., Délia, M.-L., Bergel, A., 2013. Microbial bioanodes with high salinity tolerance for microbial fuel cells and microbial electrolysis cells. Electrochem. Commun. 33, 1–4.

Rozanov, A.S., Logacheva, M.D., Peltek, S.E., 2014. Draft genome sequences of Geobacillus stearothermophilus strains 22 and 53, isolated from the Garga hot spring in the Barguzin River valley of the Russian Federation. Genome Announce. 2 (6), e01205–14.

Rozanov, A.S., Sushentseva, N.N., Malup, T.K., Goryachkovskaya, T.N., Demidova, E.V., Meshcheriakova, I.A., Demidov, E.A., Peltek, S.E., 2015. Analysis of enzymes of the hemicellulose complex from Geobacillus stearothermophilus 22 VKPM B-11678 isolated from Garga hot spring, Russia. J. Mol. Catal. B: Enzym. 116, 159–165.

Scharf, B., Wittenberg, R., Engelhard, M., 1997. Electron transfer proteins from the haloalkaliphilic archaeon Natronobacterium pharaonis: possible components of the respiratory chain include cytochrome bc and a terminal oxidase cytochrome ba 3. Biochemistry 36 (15), 4471–4479.

Shehab, N.A., Ortiz-Medina, J.F., Katuri, K.P., Hari, A.R., Amy, G., Logan, B.E., Saikaly, P.E., 2017. Enrichment of extremophilic exoelectrogens in microbial electrolysis cells using Red Sea brine pools as inocula. Bioresour. Technol. 239, 82–86.

Shrestha, N., 2017. Microbially assisted capacitive deionization cell for desalination of oil and gas wastewaters from tight oil production (MS Thesis). Civil and Environmental Engineering. South Dakota School of Mines and Technology.

Shrestha, N., Chilkoor, G., Wilder, J., Gadhamshetty, V., Stone, J.J., 2017a. Potential water resource impacts of hydraulic fracturing from unconventional oil production in the Bakken shale. Water Res. 108, 1–24.

Shrestha, N., Tripathi, A., Rauniyar, S., Sani, R., Gadhamshetty, V. 2017b. Electrochemical activity of Geobacillus sp. strain WSUCF1 under thermophilic conditions (Unpublished work).

Shrestha, N., Tripathi, A., Rauniyar, S., Sani, R., Gadhamshetty, V. 2017c. Electrochemical activity of Geobacillus sp. strain WSUCF1 under thermophilic conditions. https://meetings.undergroundphysics.org/indico/contributionDisplay.py?contribId = 59&sessionId = 13&confId = 1. (accessed November, 2017).

Shrestha, N., Chilkoor, G., Wilder, J., Ren, Z.J., Gadhamshetty, V., 2018. Comparative performances of microbial capacitive deionization cell and microbial fuel cell fed with produced water from the Bakken shale. Bioelectrochemistry.

Shukla, G., Pandey, R.P., Shahi, V.K., 2016. Temperature resistant phosphorylated graphene oxide-sulphonated polyimide composite cation exchange membrane for water desalination with improved performance. J. Membr. Sci. 520, 972–982.

Siddiqui, M.A., Rashid, N., Ayyampalayam, S., Whitman, W.B., 2014. Draft genome sequence of Geobacillus thermopakistaniensis strain MAS1. Genome Announce. 2 (3), e00559–14.

Singh, N.K., Carlson, C., Sani, R.K., Venkateswaran, K., 2017. Draft Genome Sequences of Thermophiles Isolated from Yates Shaft, a Deep-Subsurface Environment. Genome

Announce. 5 (22), e00405–17.

Singh, O.V., 2012. Extremophiles: Sustainable Resources and Biotechnological Implications. John Wiley & Sons.

Sorokin, D.Y., Kublanov, I.V., Yakimov, M.M., Rijpstra, W.I.C., Damsté, J.S.S., 2016. Halanaeroarchaeum sulfurireducens gen. nov., sp. nov., the first obligately anaerobic sulfur-respiring haloarchaeon, isolated from a hypersaline lake. Int. J. Syst. Evolut. Microbiol. 66 (6), 2377–2381.

Stan-Lotter, H., Fendrihan, S., 2012. Adaption of Microbial Life to Environmental Extremes. Springer, Vienna New York.

Tenchov, B., Vescio, E.M., Sprott, G.D., Zeidel, M.L., Mathai, J.C., 2006. Salt tolerance of archaeal extremely halophilic lipid membranes. J. Biol. Chem. 281 (15), 10016–10023.

Tindall, B.J., Schneider, S., Lapidus, A., Copeland, A., Del Rio, T.G., Nolan, M., Lucas, S., Chen, F., Tice, H., Cheng, J.-F., 2009. Complete genome sequence of Halomicrobium mukohataei type strain (arg-2T). Standards Genom. Sci. 1 (3), 270–277.

Tiwari, A., Pandey, A., 2012. Cyanobacterial hydrogen production–a step towards clean environment. Int. J. Hydrogen Energy 37 (1), 139–150.

van de Vossenberg, J.L., Driessen, A.J., Konings, W.N., 1998. The essence of being extremophilic: the role of the unique archaeal membrane lipids. Extremophiles 2 (3), 163–170.

Wang, H., Ren, Z.J., 2013. A comprehensive review of microbial electrochemical systems as a platform technology. Biotechnol. Adv. 31 (8), 1796–1807.

Wang, Q., Cen, Z., Zhao, J., 2015. The survival mechanisms of thermophiles at high temperatures: an angle of omics. Physiology 30 (2), 97–106.

Wegener, G., Krukenberg, V., Riedel, D., Tegetmeyer, H.E., Boetius, A., 2015. Intercellular wiring enables electron transfer between methanotrophic archaea and bacteria. Nature 526 (7574), 587–590.

Wiegand, S., Rabausch, U., Chow, J., Daniel, R., Streit, W.R., Liesegang, H., 2013. Complete genome sequence of Geobacillus sp. strain GHH01, a thermophilic lipase-secreting bacterium. Genome Announce. 1 (2), e00092–13.

Wildgoose, G.G., Giovanelli, D., Lawrence, N.S., Compton, R.G., 2004. High-temperature electrochemistry: a review. Electroanalysis 16 (6), 421–433.

Wrighton, K., Thrash, J., Melnyk, R., Bigi, J., Byrne-Bailey, K., Remis, J., Schichnes, D., Auer, M., Chang, C., Coates, J., 2011. Evidence for direct electron transfer by a Gram-positive bacterium isolated from a microbial fuel cell. Appl. Environ. Microbiol. 77 (21), 7633–7639.

Wrighton, K.C., Agbo, P., Warnecke, F., Weber, K.A., Brodie, E.L., DeSantis, T.Z., Hugenholtz, P., Andersen, G.L., Coates, J.D., 2008. A novel ecological role of the Firmicutes identified in thermophilic microbial fuel cells. ISME J. 2 (11), 1146–1156.

Xiao, L., He, Z., 2014. Applications and perspectives of phototrophic microorganisms for electricity generation from organic compounds in microbial fuel cells. Renew. Sust. Energy Rev. 37, 550–559.

Xu, F., Duan, J., Hou, B., 2010. Electron transfer process from marine biofilms to graphite electrodes in seawater. Bioelectrochemistry. 78 (1), 92–95.

Xu, F., Mou, Z., Geng, J., Zhang, X., Li, C.-Z., 2016. Azo dye decolorization by a halotolerant exoelectrogenic decolorizer isolated from marine sediment. Chemosphere 158, 30–36.

Yin, J., Chen, J.-C., Wu, Q., Chen, G.-Q., 2015. Halophiles, coming stars for industrial biotechnology. Biotechnol. Adv. 33 (7), 1433–1442.

Zeldovich, K.B., Berezovsky, I.N., Shakhnovich, E.I., 2007. Protein and DNA sequence determinants of thermophilic adaptation. PLoS Comput. Biol. 3 (1), e5.

Zhang, F., Yang, J.-H., Dai, K., Chen, Y., Li, Q.-R., Gao, F.-M., Zeng, R.J., 2016. Characterization of microbial compositions in a thermophilic chemostat of mixed culture fermentation. Appl. Microbiol. Biotechnol. 100 (3), 1511–1521.

Zhuang, L., Yuan, Y., Wang, Y., Zhou, S., 2012. Long-term evaluation of a 10-liter serpentine-type microbial fuel cell stack treating brewery wastewater. Bioresour. Technol. 123, 406–412.

Zinadini, S., Zinatizadeh, A., Rahimi, M., Vatanpour, V., Rahimi, Z., 2017. High power generation and COD removal in a microbial fuel cell operated by a novel sulfonated PES/PES blend proton exchange membrane. Energy 125, 427–438.