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REVIEW

Nature and bioprospecting of haloalkaliphilics: a review

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Abstract

The haloalkaliphilics are an important subset of extremophiles that grow in salt [upto 33% (wt/vol) NaCl] and alkaline pH (> 9). They are found in hypersaline environments especially in the brines in arid, coastal and deep sea locations, and in alkaline environments, such as soda soils, lakes and deserts. Some authors have described haloalkaliphilic bacteria as moderate halophilic bacteria, but the molecular and classical studies revealed that they belong to moderately to extremely halophilic bacteria and archaea. Organic solutes, such as glycine, betaine and other amino acid derivatives, sugars such as, sucrose and trehalose, and sugar alcohols present in the haloalkaliphilics help for their osmoadaptation, and also serve as stabilizers. Haloalkalphilics secrete exoenzymes like proteases, amylases, xylanases, cellulases and peroxidases which have potential industrial applications. They also produce bacteriorhodopsin, compatible solutes, pigments, biopolymers, secondary metabolites like biosurfactants, polyhydroxyalkanoate (PHA) and exopolysaccharides and antimicrobial/anticancer compounds. They have unique metabolic pathways which can be used to treat industrial pollutants, heavy metals and waste water.

Keywords Haloalkaliphilics · Adaptations · Industrial products · Biomedical importance

Introduction

Alkaliphiles are microorganisms that grow at pH above 7, often between 10 and 13. Alkaliphilic bacteria exist in two physiological groups of microorganisms, namely alkaliphiles and haloalkaliphiles. For the growth, alkaliphiles require an alkaline pH of 9 or more, whereas haloalkaliphiles require both alkaline pH (> pH 9) and saline (upto 33% [w/v] NaCl) conditions. Alkaliphiles have been isolated from neutral environments, such as acidic soils and feces whereas haloalkaliphiles from extremely alkaline saline environments like soda lakes and soda deserts. The haloalkaliphiles are the representatives of halophilic archaea, red-pigmented and moderate thermophiles (grows at 40 °C). The term "natronophile" ("natron-loving" organisms or "chloride-independent sodaphile") represents the haloalkalophiles which requires Na_2CO_3/$NaHCO_3$ for their growth (Banciu 2004; Sorokin et al 2011a). Some of the natronophiles require chloride ions for their growth (Oren 2011). Based on their alkaline nature, there are different types of haloalkaliphiles like obligate (true) alkaliphiles (pH 9–11.5), facultative alkaliphiles (pH 7.5–11), alkalitolerant (pH 7.5–11), true extremely halophile/natronophile (pH 8–10.7), true moderatelyhaloalkaliphile/natronophile (pH 8–10.5), and low salt tolerant natranophile (pH 8–10.5) (Banciu and Sorokin 2013).

Chemistry of the habitat

Saline-alkaline habitats are characterized by high salinity (> 60 g/L total salinity) and high alkalinity (pH > 9). The high salinity and alkalinity to the saline-alkaline habitats are provided by Na_2CO_3 and $NaHCO_3$, and these environments are known as soda systems. The soda systems i.e., soda lakes or soda soils are located in arid and semiarid regions and are athalassic (continental). The soda system contains high concentration of Na_2CO_3, $NaHCO_3$ and NaCl and lacks the soluble divalent cations like Mg^{2+} and Ca^{2+} cations, and contains the monovalent cations in the form of Na/K carbonates. High levels of soluble inorganic phosphorous, low toxicity of sulphide and nitrite, high toxicity of ammonia are also found in soda systems and have major implications on

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microbial systems. This saline-alkaline habitat has primary biomass production because of the fully-balanced elements present in the environment. During dry seasons, the shallow soda lakes evaporates quickly leading to the formation of layer of solid rock called trona (crystalline sodium sesquihydrate, $Na_2CO_3{\cdot}NaHCO_3{\cdot}2H_2O$) (Grant and Sorokin 2011).

Saline-alkaline lakes are located in East African Rift Valley, the Eestern and Northern USA, the Middle East (Turkey, Armenia), and Central Asia (Southern Siberia, Northeastern and Inner Mongolia, China). Remote soda lakes are also located in other parts of the world, such as Australia, Central and South America (Chile, Venezuela), and southern Asia (India). Low-salt alkaline ponds and soils are found in Europe (Austria, Hungary, Serbia) (Tindall 1988). In India, the study of haloalkaliphilic bacteria occurs in the manmade and natural saline habitats along the Coastal Gujarat for many years (Patel et al. 2006; Nowlan et al. 2006; Dodia et al. 2008; Joshi et al. 2008; Pandey et al. 2012; Purohit and Singh 2012).

Biodiversity of soda environments

Brine shrimp (*Artemia* sp.,) (Sorokin et al. 2012a), zooplankton species like rotifers (e.g., *Brachionus plicatilis*), cladocerans (*Moina hutchinsoni*), and copepods (*Diaptomus sicilis*) (Bozek 1989), cyanobacteria from the genera *Arthrospira* sp., *Cyanospira* sp., *Synechococcus* sp., and *Synechocystis* sp. (Grant et al. 1990), *Ectothiorhodospira* and *Halorhodospira* (Grant and Tindall 1986), are found in soda environments. Haloalkaliphilic bacteria and archaeon found in hypersaline environments are listed in Tables 1 and 2.

Adaptation of haloalkaliphilies cell envelope

Phospholipid and fatty acid composition in the cell envelope

The polar phospholipids, such as phosphatidylglycerol (PG), phosphatidylethanolamine, and diphosphatidylglycerol or cardiolipin and non-polar lipids such as isoprenoids (e.g., quinones, squalene, pigments) are present in the cell envelopes (cell wall and cytoplasmic membrane) of the haloalkaliphiles, playing an important role in high salt and high pH adaptations (Banciu and Sorokin 2013).

Gram positive bacteria contain high amount of branched chain fatty acids (BFAs) whereas the Gram negative bacteria possess alicyclic fatty acids (CFAs). The most common straight-chained fatty acids found in bacteria are saturated fatty acids, such as myristic acid, palmitic acid, stearic acid, palmitoleic acid, and the monounsaturated fatty oleic acid. The 15-methylpalmitic acid and 14-methylpalmitic acid are the iso- and ante-iso-branched fatty acids found in Gram-positive bacteria (Oren 2012). From experiments on salt-stress-effect on lipid composition of various haloalkaliphilic bacteria (Vargas et al. 2005b), it was found that the membrane fluidity between the environmental factors (temperature and pH) and cell response (phospholipids and fatty acids composition) play an important role.

The alkaliphiles develop a high amount of BFAs at pH 9. A balance between anteiso- and iso-fatty acids is important in pH adaptation (Giotis et al. 2007). BFAs along with unsaturated fatty acids (UFAs) have lowest phase transition temperature ($Tm = -16.5$ °C) (Kaneda 1991) and influence membrane fluidity (Silvius 1982). The biosynthesis of UFAs occurs either aerobically or anaerobically (Aguilar and de Mendoza 2006). In the anaerobic alkaliphiles, such as members of the family Clostridiaceae (Zhu et al. 2009) and the haloalkaliphilic anaerobic bacteria (e.g., *Tindallia* sp., *Natroniella* spp., *Natronincola* spp.) contain significant amounts of UFAs.

The salt dependant cyclopropane fatty acid (CFA) synthase (converts cis-monounsaturated fatty acids like C18:1 to cyc-C19 and vice versa) present in bacteria, which regulates the membrane lipid composition and fluidity, plays an important role in the adaptation of bacteria in response to alkaline pH and high salt concentration (To et al. 2011). The raised CFA content increases the membrane rigidity (Russell 1993) and the CFAs such as cyc-C19 are considered as biomarkers for Gram-negative bacteria (Zelles 1999).

Bacterial plasmalogens also play an important role in membrane fluidity. The plasmalogens and their glycerol acetals help the plasticity of bacterial membranes, especially for the bacterial cells growing at a wide range of temperatures, salinity, and the presence of solutes such as hydrocarbons and solvents. The plasmalogens in anaerobic bacteria protect the bacterial cell against oxidative stress (Goldfine 2010).

The alkaliphilic bacteria contain high amount of squalene, anionic phospholipids, especially cardiolipin (Clejan et al. 1986) and triterpene compound lanosterol. These compounds help to lower the membrane permeability to ions (i.e., protons, sodium ions) to cope with water availability in the surroundings.

Acidic cell wall

The cell wall plays an essential role in protecting the cell against the stress caused by high salinity and alkalinity. The cell wall of Gram positive halolalkaliphilic bacteria is made up of peptidoglycan and two acidic polymers: teichuronic acid (TUA) and teichurono peptide (TUP) (Aono 1990). In certain haloalkaliphiles, the TUP is substituted by an S-layer of protein nature; a capsule made of negatively charged

Table 1 Haloalkaliphilic bacteria found in the hypersaline environments

Sl. No.	Haloalkaliphilc bacteria	References
1	*Alkalibacillus haloalkaliphilus*	Kanekar et al. (2008)
2	*Alkalilimnicola ehrlichii*	Hoeft et al. (2007)
3	*Amphibacillus jilinensis* and *Amphibacillus marinus*	Wu et al. (2009) and Ren et al. (2013)
4	*Anoxynatronum buryatiense*	Ryzhmanova et al. (2017)
5	*Bacillus alkalisediminis, B. aurantiacus, B. bogoriensis, B. chagannorensis, B. daliensis, B. halosaccharovorans, B. iranensis, B. ligniniphilus, B. locisalis, B. polygoni, B. kiskunsagensis, B. salsus, B. urumqiensis, B. qingdaonensis, B. cereus* TC-1, *B. saliphilus*	Vargas et al. (2005a), Borsodi et al. (2011, 2017), Marquez et al. (2011), Zhai et al. (2012), Zhang et al. (2016a), Wang et al. (2007), Donio et al. (2014) and El Hidri et al. (2013)
6	*Chitinispirillum alkaliphilum*	Sorokin et al. (2016)
7	*Desulfohalophilus alkaliarsenatis*	Switzer Blum et al. (2012)
8	*Desulfonatronospira sulfatiphila, Desulfitispora elongate*	Sorokin and Chernyh (2017)
9	*Desulfonatronovibrio hydrogenovorans*, *D. thiodismutans, D. halophilus*	Zhilina et al. (1997) and Sorokin et al. (2011c, 2012b)
10	*Fuchsiella alkaliacetigena*	Zhilina et al. (2012)
11	*Halanaerobium hydrogeniformans*	Mormile (2014)
12	*Halobacterium pharaonis*	Soliman and Truper (1982)
13	*Halolactibacillus alkaliphilus*	Cao et al. (2008)
14	*Halomonas alkaliantarctica*, *H. campaniensis*, *H. alkaliphila*, *H. campisalis*, *H. boliviensis*, *H. magadiensis*, *H. kenyensis*, *H. mongoliensis*	Mormile et al. (1999), Quillaguaman et al. (2004), Romano et al. (2006), Poli et al. (2007), Duckworth et al. (1996, 2000) and Shapovalova et al. (2008)
15	*Heliorestis* sp.	Asao et al. (2006)
16	*Methylomicrobium buryatense, M. alcaliphilum*, *M. kenyense*	Kaluzhnaya et al. (2001, 2008)
17	*Methylophaga alcalica*, *M. aminisulfidivorans*, *M. natronica*, *Methylohalomonas lacus*, *M. lonarensis*, *Methylonatronum kenyense*	Doronina et al. (2003a, b), Antony et al. (2012), Sorokin et al. (2007a, b, c) and Trotsenko et al. (2007)
18	*Natranaerobius thermophilus*, *N. trueperi,* and *Natronovirga wadinatrunensis*	Mesbah and Wiegel (2009)
19	*Natroniella acetigena, N. sulfidigena, Natronoincola histidinovorans*	Zhilina et al. (1996), Sorokin et al. (2011b) and Zhilina et al. (1998)
20	*Natronobiforma cellulositropha*	Sorokin et al. (2018)
21	*Nocardiopsis* spp. AJ1, AJ2, AJ3, AJ4, AJ5 and AJ6 and *Streptomyces* sp. AJ7, AJ8, AJ9 and AJ10	Jenifer et al. (2013)
22	*Oceanobacillus* spp.	Tambekar and Dhundale (2013) and El Hidri et al. (2013)
23	*Proteinivorax tanatarense* and *Proteinivorax hydrogeniformans*	Kevbrin et al. (2013) and Boltyanskaya et al. (2018)
24	*Salinivibrio costicola* subsp. *alcaliphilus*	Romano et al. (2005)
25	*Salsuginibacillus kocurii* and *S. halophilus*	Carrasco et al. (2007) and Cao et al. (2010)
26	*Spirochaeta alkalica*, *S. africana*, *S. asiatica*, *S. americana*, and *S. dissipatitropha*	Zhilina et al. (1996), Hoover et al. (2003) and Pikuta et al. (2009)
27	*Streptomyces* spp. AJ8, *Streptomyces castaneoglobisporus* AJ9	Jenifer et al. (2015, 2018)
28	*Thioalkalimicrobium aerophilum, T. sibericum, Thioalkalivibrio versutus, T. nitratis, T. denitrificancs*, *Thioalkalimicrobium cyclicum, Thioalkalivibrio jannaschii*	Sorokin et al. (2001a, b) and Sorokin (2002)
29	*Thiorhodospira sibirica*, *Thioalkalicoccus limnaeus*	Bryantseva et al. (2000)

poly- γ—D -glutamate is anchored to the outer surface of the S-layer (Janto et al. 2011).

Organic compatible solutes

Haloalkaliphiles use the compatible solutes to balance the external osmotic pressure. Organic osmotic solutes reduce the osmotic adaptation by producing smaller organic compatible solutes, such as glycerol, glycine betaine, and ecotine. Glycerol can be used as organic solute only by the eukaryotic microorganisms, algae such as *Dunaliella* spp. and *Asteromonas* spp. (Ben-Amotz and Avron 1980), alkaliphilic halobacteria *Natronococcus* spp. and *Natronobacterium* spp. (Desmarais et al. 1997; Goh et al. 2011; Youssef et al. 2014). The organic compatible solutes are also applied in cosmetology, agriculture and medicine.

Table 2 Haloalkaliphilic archaeon found in hypersaline environments

Sl. No.	Haloalkaliphilic archaeon	References
1	*Halalkalicoccus tibetensis*	Xue (2005)
2	*Natrarchaeobius chitinivorans, Natrarchaeobius halalkaliphilus*	Sorokin et al. (2019)
3	*Natrialba hulunbeirensis, Natrialba chahannaoensis*	Xu et al. (2001)
4	*Natronobacterium gregoryi, N. magadii, N. pharaonis, Natronococcus occultus*	Tindall et al. (1984)
5	*Natronobacterium nitratireducens*	Xin et al. (2001)
6	*Natronolimnobius baerhuensis* and *N. innermongolicus*	Itoh et al. (2004)
7	*Natronorubrum sediminis*	Gutierrez et al. (2009)
8	*Natronorubrum sulfidifaciens*	Cui et al. (2007)
9	*Natronorubrum texcoconense*	Ruiz-Romero et al. (2012)
10	*Natronorubrurn bangense, Natronorubrurn tibetense*	Xu et al. (1999)

Glycine betaine, or simply betaine, is a trimethylated derivative of glycine: a highly polar, low molecular weight and chemically inert molecule used as osmoprotectant in all the three domains of life (Lim et al. 2007; Tuteja 2007; Oren 2008). Glycine betaine was synthesized from *Desulfonatronospira thiodismutans* ASO3-1 (Sorokin et al. 2008a), *Natranaerobius thermophilus, Thioalkalivibrio versutus* ALJ 15 (Banciu et al. 2005), *Desulfonatronospira thiodismutans* ASO3-1 (Sorokin et al. 2008a), *Halomonas elongata* and *Methanohalophilus portucalensis, Halobacillus halophillus*, *Thioalkalivibrio versutus* (Purohit and Singh 2012), *Thiohalorhabdus denitrificans* and *Thiohalospira halophila*. Glycine betaine was also synthesized from the moderately halophilic and facultatively alkaliphilic *Thiohalospira alkaliphila* (Sorokin et al. 2008a, c), *Halorhodospira halochloris*, *Ectothiorhodospira marismortui*, *Ect. haloalkaliphila* (Galinski and Herzog 1990; Imhoff 1993), and from the haloalkalitolerant cyanobacterium *Aphanothece halophytica* (Laloknam et al. 2006).

Ectoine (1,4,5,6-tetrahydro-2-methyl-4-pyrimidine carboxylic acid) is a derivative of aspartate. The organic solute ectoine is synthesized in salt stressed conditions, and the stressed conditions such as elevated temperature trigger hydroxylation of some ectoine to form hydroxyectoine. Ectoine and hydroxyectoine are involved in osmoprotection of salt-stressed cells, required for heat- and cold-shock adaptation of bacterial cells (Bursy et al. 2008; Kuhlmann et al. 2011). Ectoine is present in the fluidity of the cell membrane (Harishchandra et al. 2010) and acts as nitrogen storage compound, as carbon and/or energy source (Galinski and Herzog 1990; Khmelenina et al. 1999; Vargas et al. 2006). Hydroxyectoine has protective and stabilizing effects on proteins including enzymes (Lippert and Galinski 1992; Borges et al. 2002).

Ectoine is produced from *Halorhodospira halochloris* (Galinski et al. 1985), haloalkaliphilic SOB from the genera *Thioalkalimicrobiumi* sp. and *Thioalkalibacter* sp. (Banciu et al. 2005, 2008), *Methylomicrobium alcaliphilum*, *Methylophaga natronica*, *M. alcalica*, and *M. lonarensis* (Trotsenko and Khmelenina 2002; Doronina et al. 2003a, b; Trotsenko et al. 2007; Antony et al. 2012), *Methylophaga alcalica* M39^{T} (Doronina et al. 2003b), *Methylophaga lonarensis* MPL^{T} (Antony et al. 2012), *Thioalkalimicrobium aerophilum* AL3^{T} (Banciu et al. 2005), *Methylophaga murata* Kr3^{T} (Doronina et al. 2005), and *Methylophaga natronica* Bur2^{T} (Doronina et al. 2003a).

Sucrose and trehalose are expensive compatible solutes, and are synthesized in salt-stressed cells. Sucrose was synthesized in *Desulfonatronovibrio* (Sorokin et al. 2011c) and in *Thioalkalivibrio* (Banciu et al. 2005). Trehalose is used as osmoprotection, as thermolyte and as antidrying agent (Mackay et al. 1984; Alarico et al. 2005; Roberts 2000). It is synthesized in *Bacillus* species (*Bacillus halodurans*, *B. clausii*, *B. selenitireducens*, and *B. pseudofirmus*), as well as in *Oceanobacillus iheyensis* and *Halobacillus halophilus* (Rimmele and Boos 1994; Helfert et al. 1995).

Cytoplasm of haloalkaliphiles

The cytoplasmic pH in haloalkaliphiles depends on primary and secondary proton transporters. The primary proton transporters are proton extruding complexes of the respiratory chain, and the secondary proton transporters are antiporters. There are five families of Na^+/H^+ antiporters. pH homeostasis is accomplished by a variety of Na^+/H^+ antiporters (Krulwich et al. 2011). A large hetero-oligomeric Mrp antiporter that extrudes Na^+ (K^+ or Li^+) in exchange for H^+ has a crucial role for survival at high pH (Ito et al. 2001; Morino et al. 2010).

A full Mrp-like complex (Ap–MrpA–G) with Na^+/H^+ and Li^+/H^+ antiport activity (Fukaya et al. 2009) which contributes to the Na^+-dependent HCO_3^- uptake, pH-regulated Na^+/H^+ antiporter, is active at alkaline pH (Wutipraditkul et al. 2005).

K^+ transporter NhaPs belonging to the monovalent cation/proton antiporter-1 (CPA1) family and members of the

K^+ transporter (Trk) family contribute to pH and K^+ homeostasis of haloalkaliphiles (Wei et al. 2007).

NaChBac homologues found in bacteria living in alkaline niches (Ito et al. 2004; Koishi et al. 2004) contribute to a significant role in the cytoplasmic ion homeostasis (Ito et al. 2004; Fujinami et al. 2007).

The main source of inorganic carbon in soda lakes is HCO_3^-, and is less accessible at alkaline pH. Therefore, the soda lake autotrophs depend on active transport of bicarbonate ion. In cyanobacteria present in soda lakes, light energy drives the uptake of CO_2 and HCO_3^- (Kaplan et al. 2008). Two CO_2 uptake systems bound to thylakoids, and three HCO_3^- transporters located in the plasma membrane covering the entire range of inorganic carbon availability are found in haloalkalophilic cyanobacteria. Two membrane transporters for bicarbonate are sodium-dependent: the inducible, high-affinity HCO_3^-/SO_4^{2-} transporter, SbtA (Shibata et al. 2002), and low-affinity, high- flux HCO_3^- transporter, BicA (Price 2011). SbtA works at low bicarbonate and high sodium concentration.

Membrane pigments

The pigments such as bacteriochlorophylls, carotenoids and rhodopsins produced by the haloalkaliphiles are able to protect high-light/UV rays and prevent oxidative-stress damages.

Natronochrome and chloronatronochrome, two yellow pigments, which were chemically characterized from the natronophile *Thioalkalivibrio versutus* (Takaichi et al. 2004), yellow-membrane-bound pigments, have been extracted from the SOB *Thiohalospira* spp. (Sorokin et al. 2008a). Xanthomonadin, a structurally related yellow pigment was isolated from the outer membrane of the *Xanthomonas* spp., (Rajagopal et al. 1997; Poplawsky et al. 2000).

Bacteriorhodopsin and halorhodopsin are membrane bound retinal pigments found in some haloalkaliphilic bacteria and haloalkaliphilic archaea. Thirty eight haloalkalihilic bacteria isolated from alkaline salt lake in Kenya and Wadi Natrun Bivin, Egypt were found to have two retinal pigments P_r and P_s (Bivin and Stoeckenius 1986). Two novel membrane-bound yellow pigments natronochrome and chloronatronochrome were extracted from the natronoalkaliphic SOB *Thioalkalivibrio versutus* strain ALJ 15 (Takaichi et al. 2004). From the strain Omega belonging to recently established phylum Balneolaeota, forming a new genus and species “Ca. *Cyclonatronum proteinivorum*” a gene encoding proteorhodopsin was discovered by Sorokin et al. (2018). Halorhodopsin (hR) was isolated and characterized from mutant strain KM-1 belonging to extremely haloalkaliphilic archaeon *Natronomonas pharaonis* strain DSM2160^T (Ihara et al. 2008).

Exoenzymes

Protease

Alkaline proteases are industrially important hydrolytic enzymes which used in various industrial products and processes, such as detergents, pharmaceuticals, leather, meat tenderizers, protein hydrolyzates, food products, waste processing, bioremediation mixes and also probiotics in aquaculture. The exoenzyme protease was found in haloalkaliphilic bacteria, such as *Salinivibrio costicola* 18AG^T (Romano et al. 2005), 8 moderate haloalkaliphilic bacteria from hypersaline habitats from the Saurashtra region of the coastal Gujarat (Dodai et al. 2006), *Bacillus* sp. strain Ve1, *Bacillus* sp. Po2 (Patel et al. 2006) and *Bacillus* sp. AH-6 (Dodia et al. 2008). Thirty eight haloalkaliphilic bacteria from Sambar lake, India (Kumar et al. 2012), alkaliphilic *Bacillus* sp. NPST-AK15 from sediment and water samples collected from hyper saline soda lakes in Wadi El-Natrun Valley, Egypt (Ibrahim et al. 2015), 16 isolates from Khewra salt mine, Pakistan (Mukhtar et al. 2018) are screened for their proteolytic activity and found to contain protease activity.

Haloalkaliphilic archaea, such as *Natronomonas pharaonis* (Stan-Lotter et al. 1999), *Natronococcus occultus* (Studdert et al. 1997, 2001), *Natrialba magadii* (Gimenez et al. 2000; de Castro et al. 2008), and *Halogeometricum borinquense* strain TSS101 (Vidyasagar et al. 2006) are also protease producers.

The haloalkaliphilic actinomycetes *Nocardiopsis* spp. AJ1, AJ6 and *Streptomyces* sp. AJ9 isolated from Puthalam saltworks, Kanyakumari District showed protease activity (Jenifer et al. 2013).

Amylase

Alkaline amylases find wide applications in textile, detergent, pharmaceutical, food and other fields. Extracellular α-amylase were screened from *Natronococcus* sp. strain Ah-36, a haloalkaliphilic archaea (Kobayashi et al. 1992), α-amylase I and α-amylase II from the haloalkaliphilic bacterial strain *Chromohalobacter* sp. TVSP 10 (Prakash et al. 2009), haloalkaliphilic bacterium EMB4 from Sambar Lake, India (Kumar et al. 2012) and 16 isolates from Khewra salt mine, Pakistan (Mukhtar et al. 2018). The haloalkaliphilic actinomycetes *Nocardiopsis* sp AJ1, AJ5, AJ6 and *Streptomyces* spp. AJ9 isolated from Puthalam saltworks, Kanyakumari District showed amylase activity (Jenifer et al. 2013).

Cellulase and xylanase

Cellulase finds applications in various industries like pulp and paper, textile, bioethanol, wine and brewery, food processing, animal feed, agriculture, detergent and waste management. The exoenzyme cellulase was screened from haloalkaliphilic bacteria such as *Clostridium alkalicellulosi* DSM 17461^T (Zhilina et al. 2005), *Streptomyces* strain (Hakobyan et al. 2013), *Bacillus subtilis* SV1 (Nargotra et al. 2016), *Staphylococcus* spp. strain SG-13 (Gupta et al. 2000), *Bacillus pumilus* GESF-1(Menon et al. 2010), *Alkalitalea saponilacus* SC/BZ-SP2^T (Zhao and Shulin 2011), 14 haloalkaliphiles isolated from Khewra salt mine, Pakistan (Mukhtar et al. 2018) and from halophilic archaea *Halorhabdus utahensis* (Zhang et al. 2011). The haloalkaliphilic actinomycetes *Streptomyces* sp. AJ8 also produces xylanase (Jenifer et al. 2013).

Lipase

Lipases find potential applications in the food, detergent, pharmaceutical, leather, textile, cosmetic, and paper industries. Exoenzyme lipase was screened from haloalkaliphilic bacterium D-10-102 isolated from Nagoa, S-15-9 from Somnath, Ve2-20-92 from Veraval (Kumar et al. 2012), 22 isolates from Khewra salt mine, Pakistan (Mukhtar et al. 2018). The haloalkaliphilic actinomycetes *Streptomyces* sp-AJ10 isolated from Puthalam saltworks, Kanyakumari District showed lipase activity (Jenifer et al. 2013).

Secondary metabolites

The secondary metabolites have many activities like pharmaceuticals, cosmetics, food agriculture and farming. The secondary metabolite compounds have activities like anti-inflammatory, hypertensive and anti-tumour. One haloalkaliphilic actinomycete isolate HA15 isolated from the saline soil samples collected from the saline desert of Kutch produced antimicrobial agents (Thamar and Pethani 2013). Jenifer et al. (2015, 2018, 2019) isolated secondary metabolites from haloalkaliphilic actinomycetes *Streptomyces* spp. AJ8, *Streptomyces castaneoglobisporus* AJ9 and *Nocardiopsis lucentensis* AJ1. The literature pertaining to the secondary metabolites in haloalkaliphiles is very scarce and more research is needed in this area.

Biosurfactant

Biosurfactants are surfactants that produce extracellularly or part of the cell membrane by bacteria, fungi and yeasts. Biosurfactants are applied in the food, environmental, cosmetic and pharmaceutical industries. A biosurfactant producing actinomycetes *Nocardiopsis* spp. B4 was isolated from the Mumbai coastal region of India (Khopade et al. 2012). Twelve biosurfactant producing haloalkaliphilic archaea were isolated from Soda Lakes of Wadi An Natrun, Egypt (Selim et al. 2012). A lipopeptide biosurfactant was isolated from the haloalkaliphilic bacteria *Bacillus atrophaeus* 5-2a and the surfactant was used to enhance oil recovery (Zang et al. 2016). The literature regarding the isolation of biosurfactant from haloalkaliphiles is very scarce.

Bio-remediation and bio-degradation

Haloalkaliphiles play an important role in bio-remediation and bio-degradation. The haloalkaliphilic SOB belonging to the genus *Thioalkalivibrio* spp. biotransformed sulphide completely into sulphate (de Graaff et al. 2011). *Thioalkalivibrio* spp. and *Halomonas* strains (Olguin-Lora et al. 2011), haloalkaliphilic SOB belong to the genus *Thioalkalivibrio* spp. (Sorokin et al. 2008b), sulphate-reducing bacteria (SRB) belong to the genus *Desulfonatronum* and the genus *Desulfonatronovibrio* (Sorokin et al. 2011c) have play a significant role in bio-remediation. Several haloalkaliphilic bacteria, *Halomonas nitrilicus*, *Marinospirillum* spp., *Bacillus alkalinitrilicus*, *Natronocella acetinitrilica*, and *Nitriliruptor alkaliphilus*, used aceto-, propio-, butyro-, isobutyro-, and valero-nitriles as carbon, energy, and nitrogen sources via nitrile hydratase/amidase pathway, have been isolated (Sorokin et al. 2007a, b, , 2008c). Thiocyanate-oxidizing bacteria belonging to SOB genus *Thioalkalivibrio* (Sorokin et al. 2001a, 2010) and the haloalkaliphilic bacterium *Thialkalivibrio thiocyanodenitrificans* ARhD 1^T anaerobically oxidized thiocyanate (Sorokin et al. 2004) have been isolated. Singh et al. (2010) screened haloalkaliphilic bacteria isolated from Coastal sea water, Gujarat which utilized polyaromatic hydrocarbons.

Staphylococcus arlettae (SDT1) and *Staphylococcus* species (SDT2) isolated from Lonar lake, Maharastra were found to degrade 64% and 75% phenol at laboratory level (Tambekar et al. 2013). *Halomonas nitrilicus* sp. nov. haloalkaliphilic bacteria isolated from sediment sample from Kulunda Steppe (South-western Siberia, Altai, Russia) biodegraded and utilized a broad range of acrylaliphatic nitriles (Chmura et al. 2008). Three haloalkaliphilic stains isolated from alkali lake and west alkali lake in the high desert of southwestern Oregon degraded 2,4-dichlorophenoxy acetic acid (Maltseva et al. 1996).

Conclusion

Haloalkaliphiles are interesting extremophiles living in high salt and alkaline conditions. There are many unexplored areas in haloalkaliphiles, such as exoenzymes, secondary metabolite production, pigment production, bio-remediation and bio-degradation. By sequencing the biosynthetic gene clusters like Non Ribosomal Peptide Synthetase (NRPS) and Polyketide Synthese (PKS) from haloalkaliphilics, the functional informations from the genome shall be obtained. The biosynthetic gene clusters encompass a wide array of clinically important drugs and have proved to be extremely powerful in expanding the repertoire of natural product libraries, hence potentially leading to the discovery of new drugs. Moreover, by utilizing the metagenomic sequencing of the microbiome saline environment, novel uncultivable microbes shall be isolated and identified, that will eventually help to explore many novel bio-active products. This area will give more scope to the scientific community.

Compliance in ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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