

Haloalkaliphilic *Bacillus* species from solar salterns: an ideal prokaryote for bioprospecting studies

Syed Shameer¹

Received: 23 December 2015 / Accepted: 26 May 2016 / Published online: 13 June 2016
© Springer-Verlag Berlin Heidelberg and the University of Milan 2016

Abstract Bioprospecting is an umbrella term describing the process of search and discovery of commercially valuable new products from biological sources in plants, animals, and microorganisms. In a way, bioprospecting includes the exploitative appropriation of indigenous forms of knowledge by commercial actors, as well as the search for previously unknown compounds in organisms that have never been used in traditional ways. These resources may be used in industrial applications, environmental, biomedical, and biotechnological aspects. *Bacillus* species are one of the most studied organisms from different perspectives and diverse environments, namely for industrial and environmental applications owing to the adaptations and versatile molecules they produce. The ability of different species to ferment in the acid, neutral, and alkaline pH ranges, combined with the presence of thermophiles in the genus, has led to the development of a variety of new commercial enzyme products with the desired temperature, pH activity, and stability properties to address a variety of specific applications. Unlike other microbial species *Bacillus* species have been isolated from different sources both natural and artificial sources some being extreme in nature, for bioprospecting studies to exploit them to fabricate novel biomolecules or functions. Solar salterns are among the least documented environments as a source of *Bacillus* species due to their unique nature comprising multiple extremities of varying degrees, namely temperature, pH, and minimal nutrients along with saturating salinity. Haloalkaliphilic *Bacillus* species are the group specifically adapted to grow

optimally under moderate halophilic and alkaline conditions. Artificial solar salterns are not evenly established as a habitat because they are created and maintained by humans. Hence, the present paper makes an attempt to review the potential of haloalkaliphilic *Bacillus* species from manmade solar salterns for bioprospecting studies.

Keywords Haloalkaliphilic *Bacillus* species · Artificial Solar salterns and Bioprospecting

Introduction

The seas that cover nearly 70 % of the surface of planet Earth contain about 35 g/L⁻¹ dissolved salt. Hypersaline environments are easily formed when seawater dries up in coastal lagoons and salt marshes, as well as in manmade evaporation ponds of saltern systems built to produce common salt by evaporation of seawater. There are also inland saline lakes in which the salt concentrations can reach close to saturation. Well-known examples are the Great Salt Lake, UT, USA, a lake in which the ionic composition of the salts resembles that of seawater, and the Dead Sea on the border between Israel and Jordan, a lake dominated by magnesium rather than by sodium as the most abundant cation. Furthermore, there are extensive underground deposits of rock salt that originated by the drying of closed marine basins. All of these environments, as well as others such as saline soils, provide a habitat for salt-adapted microorganisms, obligate halophiles, as well as halotolerant organisms that can adjust to life over a wide range of salt concentrations.

Solar salterns are hypersaline water bodies located along the sea-coast and are the main source of salt generated through the evaporation of seawater. They are generally composed of a system of shallow ponds with salinities ranging from of

✉ Syed Shameer
syeds962@gmail.com

¹ Department of Microbiology, Sri Venkateswara University, Tirupati, AP, India 517 502

seawater to supersaturated brines. These elevated saline concentrations represent extreme environmental conditions leading to the growth of only a few specialized groups of microorganisms: the halophiles. These halophilic microbial communities (Oren 2006; Pedrós-Alió 2006) are adapted to life at high salt concentrations and to the high osmotic pressure of their environment resulting from the high salinity. In addition, other factors such as temperature, pH, oxygen, nutrient availability, and solar radiation prevailing in these environments also limit the growth of microorganisms. Most of the solar salterns tend to be alkaline in nature due to carbonates, and only a negligible number are acidic in nature (those are near acidic or sulphur mines). Artificial solar salterns are unique polyextremophilic environments characterized by saturating salinities (15–35 %), moderate alkalinity pH (9.0), and mesophilic temperatures (45–50 °C), which are the conditions most prevalent in industrial processes. Another reason that artificial solar salterns are a source of potential prokaryotes is they are the dominant population when compared with eukaryotic groups such as fungi or algae (Syed et al. 2012).

Apart from Haloarchaea, *Bacillus* species are prominently found in the less saline zones of solar salterns, particularly in saturation ponds, which have 15–25 % salinity. *Bacillus* species continue to be dominant bacterial workhorses in microbial fermentations. *Bacillus subtilis* is the key microbial participant in the ongoing production of large-scale hydrolytic enzyme production, and some *Bacillus* species are on the Food and Drug Administration's GRAS (generally regarded as safe) list. The capacity of selected *Bacillus* strains to produce and secrete large quantities (20–25 g/L) of extracellular enzymes has placed them among the most important industrial enzyme producers. The *Bacillus* strains isolated from solar salterns have properties such as temperature and alkalinity tolerance of considerable level. Thus, the special natural adaptations of the *Bacillus* species from solar salterns render them ideal candidates for multiple application bioprospecting studies. This review attempts to consolidate the recent applications of haloalkaliphilic *Bacillus* species to inspire extensive study of the same to the fullest.

Halophiles

Halophiles are able to survive in salty conditions through cellular and molecular adaptations, including adjusting the cell turgor to different external salinities by controlling the concentration of protective molecules such as ectoine, betaine, and amino acids (glutamine, glutamate, proline, and glycine) by producing them intracellularly or taken up from the environment, and by concentration regulation of compatible solutes such as chloride and sodium/potassium in intracellular

environments, depending on external salinity (Müller and Köcher 2011) (Fig. 1) (Marco and Erhard 2011). Because water tends to flow from areas of high solute concentration to areas of lower concentration, a cell suspended in a very salty solution will lose water and become dehydrated unless its cytoplasm contains a higher concentration of salts than its environment. Halophiles contend with this problem by producing large amounts of an internal solute or by recollecting a solute extracted from outside (Garabito et al. 1998). Halophily refers to the ionic requirements for life at high salt concentrations. Although these phenomena are physiologically distinct, they are environmentally associated with other physiological parameters. Thus, a halophile must cope with osmotic stress (Oren 2006). Halophiles include a range of microbes, but some Archaea, cyanobacteria, and the green alga *Dunaliella salina* can withstand periods in saturated NaCl. For instance, an Archaeon known as *Halobacterium salinarum* concentrates potassium chloride in its interior. As might be expected, the enzymes in its cytoplasm will function only if a high concentration of potassium chloride is present, but proteins in *Halobacterium salinarum* cell structures that are in contact with the environment require a high concentration of NaCl.

Haloalkaliphiles

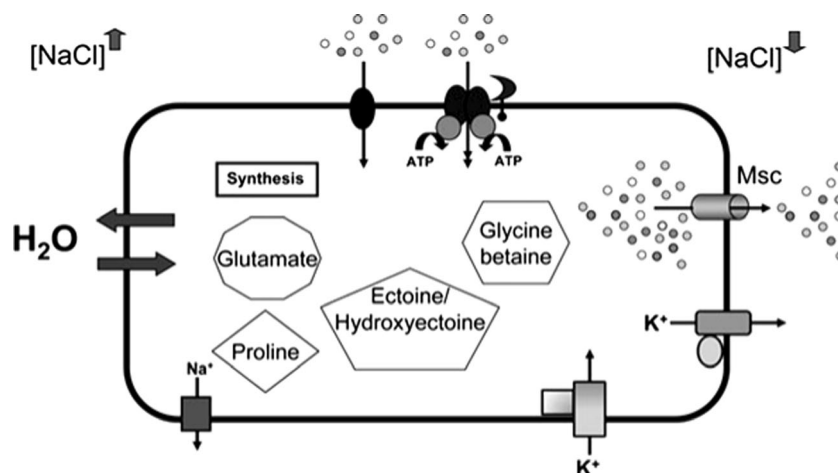
Alkaliphiles consist of two main physiological groups of microorganisms, alkaliphiles and haloalkaliphiles. Alkaliphiles require an alkaline pH of 9 or more for their growth and have an optimal growth pH of around 10, whereas haloalkaliphiles require both an alkaline pH (>pH 9) and high salinity (up to 33 % (w/v) NaCl) (Horikoshi 1996). The environments or sources for this group of microorganisms are both natural and artificial in nature (Oren 2002a).

Adaptation strategies for haloalkaliphiles

Haloalkaliphiles possess adaptation mechanisms, which include production of high density lipids with branched chains and increased content of cell wall components (glutamic acid, diaminopimelic acid, muramic acid, and glucosamine) along with the presence of poly- γ -L-glutamic acid along with Na⁺/H⁺ antiporters as internal pH homeostasis for survival in highly saline and alkaline pH (Horikoshi 2011; Krulwich et al. 2011). These properties make them interesting not only for fundamental research, but also for industrial application (Margesin and Schinner 2001; Purohit et al. 2014). So far, moderately haloalkaliphilic bacteria have been isolated from the different saline and alkaline environments (Ventosa et al. 1998; Patel et al. 2005; Xu et al. 2007).

Extremophiles adopt two distinct approaches to living within extreme environments; they adapt to function within

Fig 1 The core of osmopressure response of Bacilli. Schematic overview of the initial and sustained cellular stress responses to high salinity through the uptake of K^+ , synthesis and import of various compatible solutes and the active export of K^+ and Na^+ ions. Non-selective expulsion of ions and organic solutes occur in response to sudden osmotic downshifts via mechanosensitive channels (Msc)



the physical and chemical bounds of their environment or they maintain mesophilic conditions intracellularly, guarding against the external pressures. Among them, halophiles are an interesting class of extremophilic organisms that have adapted to harsh, hypersaline environments (Oren 2002b).

Applications of haloalkaliphiles

Stable alkaline conditions are caused by an unusual combination of climatic, geological, and topological conditions. Soda lakes represent the most stable high-pH environments on earth and commonly have pH values above 11.5. These environments are associated with a low Mg^{2+} , Ca^{2+} geology together with rates of evaporation that exceed any inflow. Transient alkalinity in microhabitats arising through biological activity such as ammonification or sulphate reduction is a widespread feature of heterogeneous environments such as soils. This is presumably the reason for the widespread presence of alkaliphiles in such environments that would be considered neutral or even acidic on the basis of bulk pH measurements (Imhoff et al. 1979).

These hypersaline alkaline brines provide the most extreme environment with a pH of around 12 and are relatively high in organic content, presumably due to evaporative concentration. Originally assigned to two genera, *Natronobacterium* and *Natronococcus*, these organisms turn out to have just as much diversity as their counterparts in pH-neutral hypersaline environments, and there are currently six genera, *Natronococcus*, *Natronobacterium*, *Natrialba*, *Halorubrum*, *Natronorubrum*, and *Natronomonas* that harbour haloalkaliphilic representatives living in these environments. The only other aerobes to have been cultivated from these environments are haloalkaliphilic *Bacillus* sp., which was distinct in having a minimum requirement of at least 15 % NaCl for growth. As might be expected from the nutrient-rich environments that they inhabit, the majority of the soda lake isolates are biochemically reactive with an arsenal of extracellular hydrolytic enzymes including

proteinases, cellulases, xylanases, and lipases (Asha et al. 2012). Two different cellulases from Gram-positive soda lake isolates are currently marketed for use in laundry and textile processes (Jones et al. 1994; Grant 2006).

Haloalkaliphilic *Bacillus* sp.

Halophilic microorganisms require very high salt (2 to 5 M NaCl) concentrations for growth and are found in salterns and hypersaline lakes. Many extreme and moderate halophiles have been isolated and investigated for possible biotechnological applications. Early literature on organisms from salted foods and solar salt interjects a running debate on the nature of adaptation to hypersaline environments. Smith (1938) reviewed the arguments, which center on whether halophilism is an evolutionary consequence or simply the adaptation of a single generation. A group of media used for enrichments of moderately halophilic and halotolerant bacteria (*Bacillus*, *Halobacillus*, *Halomonas*, *Salibacillus*, *Salinibacter*) has approximately 10 % salinity (Quesada et al. 1983; Caton et al. 2004; Sass et al. 2008).

A large body of evidence suggests that *Bacillus* species were isolated from various haloalkaline environments such as soda lake Van in Turkey and Inner Mongolian Bear soda lake (Ma et al. 2004). Recently, Tambekar and Dhundale (2012) reported the phenotypic analysis of *B. flexus*, *B. cellulosilyticus*, *B. pseudofirmus*, *B. clausii*, *B. krulwichiae*, *B. pumilus*, *B. lehensis*, *B. halodurans*, *B. circulans*, *B. cereus*, *B. agaradhaerens*, *B. sphaericus*, *B. fusiformis*, *B. asahii*, *B. pseudalcalophilus*, *B. okuhidensis*, and *B. gibsonii*.

Potential applications of Haloalkaliphilic *Bacillus* sp.

The biological diversity of the marine environment, in particular, offers enormous scope for the discovery of novel natural

products, several of which are potential targets for biomedical developments. Extremophiles have been recognized as valuable sources of novel bioproducts and this may well include antimicrobials (Horikoshi 1999; Das et al. 2014; Wu et al. 2014). These groups of prokaryotes have received considerable interest because of their potential applications in various biotechnological and industrial aspects, such as biomedical and chemical sciences, food, leather, laundry detergent, and pharmaceutical industries (Rothschild and Mancinelli 2001). Moreover, some bacterial metabolites, such as proteins, extracellular enzymes, osmotically active substances, exopolysaccharides, and special lipids have potential industrial applications (Schiraldi and De Rosa 2002; Ara et al. 2014). They appear to be a very good source of various biomolecules and can open the dimensions for the development of novel value based products because of unique properties, which can withstand at harsh environment (Saju et al. 2011; Prakash and Gopal 2014) Fig. 2.

Enzymes/biocatalysts

Haloalkaliphilic *Bacillus* sp., have the capability to produce multiple enzymes applied in multifaceted industries from food and related sectors to bioremediation of polluted environments (Fergus 1977; Adams et al. 1995). The biocatalysts from the haloalkaliphilic *Bacillus* sp. have optimal activity at moderately extreme conditions requiring presence of $\text{Na}^+\text{-Cl}^-$ for ion induced stability of the enzymes, where normal enzymes would deactivate and cease to function (Bajaj et al.

2014). The enzymes from this genus include both α and β amylases, proteases both alkali and acidic, nucleases and phosphatase, and bacteriolytic enzymes, which are able to function optimally at higher temperatures (40–60 °C), salinity (0.5–1.5 M), and alkalinity (7.0–8.5) compared with those from normal organisms (Oren 2002a; Ibrahim and El-diwany 2007; Syed et al. 2013a, b; Singh and Bajaj 2014; Annamalai et al. 2014) (Table 1).

Organic acids

During the cultivation of alkaliphiles, the pH values of culture media often decrease sharply due to the production of organic acids, which are produced by growth on carbohydrates. Paavilainen et al. (1994) reported comparative studies of organic acids produced by alkaliphilic bacilli. Four bacilli, *Bacillus* sp. strain 38–2 (ATCC 21783), *B. alkalophilus* sub sp. *Halodurans* (ATCC 27557), *B. alcalophilus* (ATCC 27648), and *Bacillus* sp. strain 17–1 (ATCC 31007), were cultured in the presence of various concentrations of sugars (1 % w/v) and related compounds such as sugar alcohols. All these alkaliphiles produced acetic acid (4.5 to 5.0 g/L at the maximum), while formic acid was produced by only one of the strains. In contrast, among neutrophilic *Bacilli*, acetoin, butanediol, and ethanol were not detected and are essentially produced as an adaptive response for fluctuating salinity gradients (Oren 2002a). Moderate amounts of isobutyric, isovaleric, α -oxo-isovaleric, α -oxo- β -methylvaleric, α -oxo-

Fig 2 Potential applications of Haloalkaliphilic *Bacillus* sp.

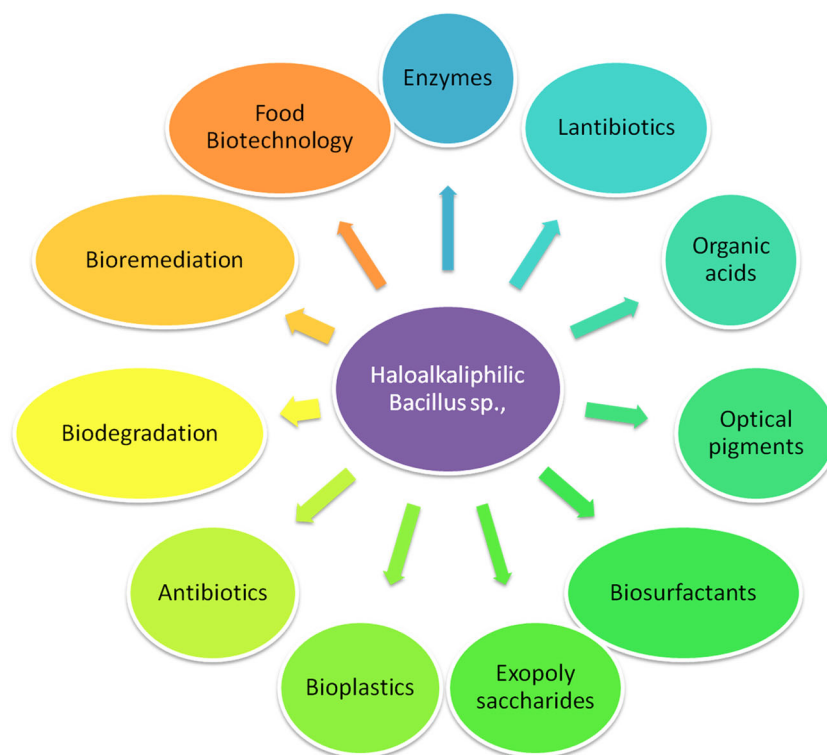


Table 1 Different Enzymes from the genus *Bacillus**

Enzyme	Species	Comments
Agarase	<i>Bacillus</i> sp.	Hydrolyzes the (β -1,4 linkage of agarose
α -Amylase	<i>B. amyloliquefaciens</i>	Endohydrolysis of the α -1,4-glucosidic linkages in polysaccharides; different species produce enzymes with different properties
	<i>B. caldolyticus</i> , <i>B. coagulans</i>	
	<i>B. licheniformis</i> , <i>B. macerans</i>	
	<i>B. stearothermophilus</i>	
	<i>B. subtilis</i> , <i>B. subtilis</i> var. <i>amylosacchariticus</i>	
β -Amylase	<i>B. cereus</i> , <i>B. megaterium</i>	Exohydrolysis of the α -1,4-glucosidic linkages in polysaccharides yielding β -maltose
	<i>B. polymyxa</i>	
	Alkalophilic <i>Bacillus</i> spp.	
Cellulase	<i>B. brevis</i> , <i>B. firmus</i> , <i>B. polymyxa</i>	Hydrolysis of carboxymethyl cellulose to cellobiose
Chitinase	<i>B. pumilus</i> , <i>B. subtilis</i>	Four enzymes induced by growth on crab-shell chitin
	<i>B. circulans</i>	
β -1,3-glucanase	<i>B. circulans</i> , <i>B. polymyxa</i>	Endohydrolysis of the β -1,3-glycosidic linkages in laminarin and related glucans
	<i>B. subtilis</i> , Alkalophilic <i>Bacillus</i> sp.	
	<i>B. amyloliquefaciens</i>	
Isoamylase	<i>B. polymyxa</i>	Hydrolysis of the α -1,6-glycosidic branch linkages in glycogen, amylopectin, etc.
Pectate lyase	<i>B. circulans</i> , <i>B. polymyxa</i>	Endocleavage of polygalacturonic acid by an eliminative reaction
	<i>B. pumilus</i> , <i>B. sphaericus</i>	
	<i>B. stearothermophilus</i>	
	<i>B. subtilis</i> ,	
	Alkalophilic <i>Bacillus</i> sp.	
Pullulanase	Alkalophilic <i>Bacillus</i> sp.	Endohydrolysis of the α -1,6 linkage of pullulan
Xylanase	<i>B. amyloliquefaciens</i>	Hydrolysis of xylans; specificity of the enzymes has not been studied in detail
	<i>B. firmus</i> , <i>B. polymyxa</i>	
	<i>B. subtilis</i> , <i>B. subtilis</i> var. <i>amylosacchariticus</i>	
Proteases		
Alkalophilic protease	Alkalophilic <i>Bacillus</i> sp.	Serine enzymes from alkalophilic species with very high pH optima
Aminopeptidase	<i>B. licheniformis</i> , <i>B. subtilis</i>	
Esterase	<i>B. subtilis</i>	Serine enzyme with high esterolytic and low proteolytic activity
Halophilic protease	<i>Bacillus</i> sp.	Produced optimally in media containing 1.0 M NaCl
Metal protease	<i>B. amyloliquefaciens</i>	Enzymes require Ca ⁺ for stability and Zn ²⁺ for activity; pH optimum at or near neutral
	<i>B. cereus</i> , <i>B. licheniformis</i>	
	<i>B. megaterium</i> , <i>B. polymyxa</i>	
	<i>B. subtilis</i> , <i>B. subtilis</i> var. <i>amylosacchariticus</i>	
	<i>B. thermoproteolyticus</i>	
	<i>B. thuringiensis</i>	
Serine protease	<i>B. amyloliquefaciens</i>	The subtilisins; alkaline pH optima, serine residue at or near the active site
	<i>B. licheniformis</i> , <i>B. pumilus</i>	
	<i>B. subtilis</i> , <i>B. subtilis</i> var. <i>amylosacchariticus</i>	
Penicillinases		
β -Lactamase	<i>B. anthracis</i> , <i>B. cereus</i>	Hydrolysis of the amide bond in the β -lactam ring of penicillins and cephalosporins
	<i>B. licheniformis</i> , <i>B. megaterium</i>	
	<i>B. subtilis</i>	

Table 1 (continued)

Enzyme	Species	Comments
Nucleases and phosphatases		
Alkaline phosphatase	<i>B. amyloliquefaciens</i> <i>B. cereus</i> , <i>B. subtilis</i>	Often cell-bound, the enzyme is extracellular in these species
Deoxyribonucleaseribonuclease	Alkalophilic <i>Bacillus</i> sp. <i>B. amyloliquefaciens</i> , <i>B. cereus</i> <i>B. pumilus</i> , <i>B. subtilis</i>	A large number of DNases, RNases, and phosphodiesterases with individual properties have been purified
3-Nucleotidase	<i>B. subtilis</i>	Active on both ribonucleotides and deoxyribonucleotides
5-Nucleotidase		Cell-bound enzyme in these species
Bacteriolytic enzymes		
Endo-N-acetylglucosaminidase	<i>B. licheniformis</i> , <i>B. subtilis</i>	
Exo-N-acetylglucosaminidase	<i>B. subtilis</i>	
Endo-N-acetylmuramidase	<i>B. subtilis</i>	True lysozyme
Exo-N-acetylmuramidase	<i>B. subtilis</i>	
N-acetyl-muramyl-L-alanine amidase	<i>B. licheniformis</i> <i>B. subtilis</i>	A cell-bound enzyme; the major autolysin
Lipase	<i>B. licheniformis</i>	Hydrolysis of triacylglycerol to diacylglycerol and a fatty acid anion
Phospholipase C	<i>B. anthracis</i> <i>B. cereus</i> <i>B. thuringiensis</i>	Responsible for the “egg-yolk” reaction
Thiaminase	<i>B. thiaminolyticus</i>	

* Source-Priest (1977)

isocaproic, and phenylacetic acids were generated by three of the alkaliphiles (Meyer et al. 2014).

Bacteriorhodopsin

Certain extremely halophilic and haloalkaliphilic bacteria contain membrane bound retinal pigments called **Bacteriorhodopsin** (BR) and **Halorhodopsin** (HR) (Lanyi 1993). The applications comprise holography, special light modulators, artificial retinas, neural networks, optical computing, and volumetric and associative memories. Recently, cloning and functional expression of the archae rhodopsin gene from *Halorubrum xinjiangense* was successfully achieved in *E. coli*, where the purple membrane was fabricated into films and photoelectric responses depending on light-on and light-off stimuli were observed (Mosin and Ignatov 2014). The presence of extreme halotolerant *Bacillus* sp. creates a great opportunity to use them as cell factories for the production of these optical pigments with less economic burden (Garabito et al. 1998).

Lantibiotics/lipopeptides

Lantibiotics or lipopeptides are small lipid molecules associated with linear or cyclic oligopeptides and other compounds and used in medicines and cosmetics for the transport of compounds to specific target sites in the body. Lipopeptides have

received considerable attention for their antimicrobial, cytotoxic, anti-tumour, immunosuppressant, and surfactant properties (Pirri et al. 2009; Raaijmakers et al. 2010; Fuchs et al. 2011; Yuan et al. 2012). The lipopeptides from *Bacillus* sp. have broad spectrum anti-microbial activity (Ongena and Jacques 2008). The ability of the *Bacillus* sp. to use different carbon sources (including cheaper ones such as paddy straw and potato peels) makes them potent candidates for lipopeptide production (Das and Mukherjee 2007; Zhu et al. 2012). Production of lipopeptides such as iturins is limited to a few species such as *B. subtilis* and *B. amyloliquefaciens*, but that of surfactin and fengycin is widespread among many *Bacillus* sp., and in that too diversity of lipopeptides and related compounds is tremendous (Mukherjee, and Das 2005; Price et al. 2007).

Biosurfactants

Biosurfactants enhance the remediation of oil-contaminated soil & water and have potential for pollution treatment in marine and coastal region (Al-Wahaibi et al. 2014; Martinez et al. 2014). *Bacillus* sp. from a variety of environments ranging from halophilic to haloalkaline are able to produce biosurfactants of multiple applications including antimicrobial, anti-adhesive agents, and enhanced oil recovery agents (Jenneman et al. 1983; Simpson et al. 2011; Joshi et al. 2012; Donio et al. 2013; Sarafin et al. 2014). Biosurfactants

from *Bacillus* species are also used for in situ Microbial Enhanced Oil Recovery (MEOR), but the production cost is a limiting factor for exploitation of these biosurfactants (Souayeh et al. 2014). To further the applications of biosurfactants, the substrates, which are cheaper, abundant, and easily available, have to be used along with statistical modelling of optimal conditions (Joshi et al. 2007; Barros et al. 2008).

Exopolysaccharides

Exopolysaccharides (EPS) are biopolymers resulting from active bacterial secretion, shedding of cell surface material, cell lysis materials, and from adsorption of organics from the environment (Wingender et al. 1999). They are composed of a variety of organic substances: carbohydrates and proteins being major constituents, with humic substances, uronic acids, and nucleic acids in smaller quantities (Liu and Fang 2002). Halophilic exopolysaccharide (EPS) producers could be interesting source for MEOR, where polymers with appropriate properties act as emulsifiers, biosorbents for metal removal or recovery, and mobility controllers (Salehizadeh and Shojaosadati 2003; Comte et al. 2006). The exopolymer poly D-glutamic acid (PGA) can be used as a biodegradable thickener, sustained release material (Zhang et al. 2014), or drug carrier in the food or pharmaceutical industries (Raliya et al. 2014). Hezayen et al. (2000) first described a PGA-producing extremely halophilic archaeon related to the genus *Natrialba*. *Bacillus* sp., in particular *B. subtilis*, *B. cereus*, *B. pumilis*, *B. coagulans*, and *B. licheniformis*, are potent producers of EPS materials as they are widely known to cope with fluctuating physiological conditions including temperature and salinity outside their cell membranes (Maugeri et al. 2002; Morikawa 2006; Marvasi et al. 2010).

Food biotechnology

Halotolerant microorganisms play an important role in various fermentation processes, occurring in the presence of salt and producing compounds that give characteristic taste, flavour, and aroma to the resulting products. In the production of pickles (fermented cucumbers), brine strength is increased by gradual increase of NaCl from 5 to 15.9 % (w/v). Certain species of halophiles; *Halobacterium salinarum*, *Halococcus* sp., *Bacillus* sp., *Pseudomonads*, and *Coryneform* bacteria are used in the production of an Asian (Thai) fish sauce, in which fish is fermented in concentrated brine (Esteban-Torres et al. 2015; Cui et al. 2015). Also related to the food industry is the commercial production of the flavoring agents 5'-guanylic acid (5'-GMP) and 5'-inosinic acid from RNA, using the halophilic nuclease H of *Micrococcus varians* subsp. *halophilus* (Kamekura and Onishi 1974). *Canthaxanthin* is used in cosmetics to decrease the necessary exposure time in sunlight to

acquire a tan and to intensify the tan as the compound attaches to the subcutaneous layer of fat (Margesin and Schinner 2001).

Metabolites produced by alkaliphilic *Bacillus*

Hamasaki et al. (1993) found that a large amount of 2-phenylethylamine was synthesized by cells of the alkaliphilic *Bacillus* sp. strain YN-2000. Most of this amine was secreted in the medium during cell growth as extracellularly released compounds where they can be extracted easily. Aono and Horikoshi (1991) reported that alkaliphilic *Bacillus* sp. strains A-40-2, 2B-2 and 57-1 produce yellow pigments in the cells and that these are triterpenoid carotenoids. Gascoyne et al. (1991) isolated a siderophore-producing alkaliphilic bacterium that accumulated iron, gallium, and aluminium. Enrichment cultures initiated with samples from a number of alkaline environmental sources yielded carotenoids (Shindo and Misawa 2014).

Bioplastics

Polyhydroxyalkanoates (PHA) is intracellularly accumulated bacterial storage molecules. Because of the unique characteristics of polyhydroxybutyrate (PHB), such as biodegradable thermo-polyester that can be produced from renewable resources and has properties similar to those of petroleum-derived plastics, they are used to replace the conventional plastics. Many *Bacillus* sp., including *B. thuringiensis*, *B. cereus*, *B. brevis*, *B. sphaericus*, *B. circulans*, *B. subtilis*, *B. licheniformis*, and *B. coagulans* are well known PHB producers (Yilmaz et al. 2005; Kumar et al. 2009). The production of PHB is essentially driven by the carbohydrate content in the medium leading to the expensive nature of its production (Yilmaz et al. 2005). *Bacillus* sp. are able to survive on a variety of carbon sources such as industrial waste, bio-wastes, and agri-wastes and are potential candidates for PHB production (Santimano et al. 2009; Quillaguamán et al. 2010). Currently, cheaper carbon and nitrogen sources, such as used vegetable oil, and low sugar carbohydrates, such as molasses and fruit peels, are employed to design novel cost effective models for production of these bioplastics (Koller et al. 2005; Verlinden et al. 2007).

Degradation of aromatic (phenols and phenolics) compounds

Hypersaline environments have both surface extension and ecological significance. As with all other ecosystems, they are impacted by pollution. However, less information is available on the biodegradation of organic pollutants by halophilic microorganisms in such environments. In addition, it is estimated that 5 % of industrial effluents are saline and hypersaline. Environmental pollution due to anthropogenic activity

has affected all types of ecosystems. Phenols and phenolic compounds are major pollutants of industrial wastes since they are commonly used in many industries such as oil refining, coke conversion, pharmaceuticals, and resin manufacturing plants. Contamination and biodegradation in extreme environments has received little attention, although many contaminated ecosystems present high or low temperatures, extreme acidic or alkaline pH, high pressure, or high salinity (Margesin and Schinner 2001). Biodegradation of phenol in hypersaline wastewaters was described by Woolard and Irvine (1994), who used a halophilic bacterial biofilm isolated from a saltern at the Great Salt Lake. More than 99 % of the phenol was removed from synthetic waste water containing 0.1 to 0.13 g/L of phenol and 15 % (w/v) NaCl in a batch-sequenced reactor. The bacteria present in the biofilm and responsible for biodegradation were not identified. Hinteregger and Streischsberg (1997) studied the biodegradation capacity of a new phenol-degrading *Halomonas* sp. strain isolated from the Great Salt Lake. Several studies have demonstrated bacterial degradation of aromatic compounds in saline conditions (Peyton et al. 2002). *Bacillus* sp., such as *B. subtilis*, *B. stearothermophilus*, *Bacillus brevis*, and *Bacillus* sp., have shown to possess the ability to degrade phenol by using it as a carbon source (Gurujeyalakshmi and Oriol 1989; Arutchelvan et al. 2006). The ability of halophiles/halotolerants to oxidize hydrocarbons in the presence of salt is useful for the biological treatment of saline ecosystems, which are contaminated with petroleum products (Margesin and Schinner 2001). However, the ecological studies concerning the ability of these microorganisms to degrade different aromatic compounds are still in their infancy.

Degradation of petroleum hydrocarbons

Petroleum hydrocarbons and their products are the origin of important pollution in almost all types of ecosystems. Atmosphere, soils, superficial and underground waters, and marine environments have been continuously affected by pollution produced during the extraction, combustion, refining, transport, and use of petroleum. There is a significant amount of literature regarding hydrocarbon biodegradation by marine microorganisms, starting with the classical reviews, such as Atlas (1981) and Colwell (1977), or more recent reviews (Swannell 1999; Harayama et al. 2004; Head et al. 2006; Chandankere et al. 2014). However, information on hydrocarbon degradation in the presence of high salt concentrations is scarce. As mentioned above, hydrocarbon biodegradation in the presence of high salt concentrations is important for the bioremediation of oil-polluted salt marshes and treatment of industrial wastewater (Fathepure 2014; Sabina et al. 2014).

Few studies of hydrocarbon degradation at high salt concentration have been carried out using axenic cultures. Bacteria as *Rhodococcus*, *Micrococcus*, and *Arthrobacter* were able to grow in a wide salinity range of 0.5 to 25 % NaCl, but hydrocarbon metabolisation was observed only up to 15 % of NaCl (Kulichevskaya et al. 1992; Zvyagintseva et al. 2001). Extreme halophilic archaea have been reported as able to metabolize hydrocarbons. *Halobacterium* sp. shows a high capacity to degrade C₁₀ - C₃₀ n-alkanes in a medium containing 30 % NaCl. Hydrocarbon co-metabolization has been reported for *H. salinarium*, *H. volcanii*, and *H. distributum* (Kulichevskaya et al. 1992).

Biosorption of heavy metals

Contamination of the environment by heavy metals is a consequence of technological and industrial processes (Volesky and Holan 1995; Abbas et al. 2010). This has led to increasing concern about the effects of toxic metals as environmental contaminants. Thus, heavy metal pollution represents an important environmental problem due to the toxic effects of metals, and their accumulation throughout the food chain leads to serious ecological and health problems (Goyer and Chisholm 1972; Nriagu 1988; Fang et al. 2014; Liu et al. 2014). Biosorption of heavy metals by microorganisms is an attractive and economical alternative method that consists of removing toxic metals from aqueous solutions based on the property of certain types of biomasses to bind and accumulate these pollutants by different mechanisms such as physical adsorption, complexation, ion exchange, and surface micro-precipitation (Kratochvil and Volesky 1998; Gutnick and Bach 2000; Ahluwalia and Goyal 2007; Mansour 2014). Halophilic and halotolerant microorganisms are suitable candidates for bioremediation processes, since they are able to grow on a wide range of salt concentrations (Hassen et al. 1998; Kratochvil and Volesky 1998; Wongsasuluk et al. 2014). The haloalkaliphiles and their products including exopolymers are used for heavy metal biosorption as they comprise charged molecules (Rudd et al. 1984; Nieto et al. 1989; Mullen et al. 1989; Rani et al. 2000; Bai et al. 2014). Syed and Paramageetham (2015) reported that the *Bacillus* sp. from solar salterns were able to remove 90 % of lead from aqueous solution.

Degradation of reactive dyes

Synthetic dyes are widely used in such industries as textile, cosmetic, printing, drug, and food processing units (Padamavathy et al. 2003). The release of coloured waste water is a problematic reality for a variety of industrial sectors. Among these are effluents released from textile and printing processes, dry cleaning, tanneries, food industries, manufacture of paints and varnishes, manufacture of plastics, and a

variety of chemical processes. Insufficient treatment of wastes or effluents released from the production process of textiles can cause grave environmental pollution, sometimes to levels that can threaten human health, livestock, wildlife, aquatic life, and collapse the entire ecosystem (Pearce et al. 2003).

Conventional treatment methods such as activated sludge process, chemical coagulation, electro-chemical treatment, chemical oxidation, carbon absorption, photo decomposition, reverse osmosis, or hydrogen peroxide catalysis are difficult, ineffective, or economically disadvantageous methods for the decolourization of reactive dyes (Gong et al. 2005; Shah et al. 2013a, b, c). Hence, the treatment of dyes focus on the involvement of some microorganisms that are able to degrade and biosorb dye in waste water. *Bacillus* species particularly haloalkaliphilic in nature are rigorously employed in the decolourisation process (Wong and Yuen 1996;

Vijayaraghavan and Yun 2008; Shyamala et al. 2014; Maulin et al. 2014). Different *bacillus* species applied in bioremediation and biodegradation of different environmental pollutants are presented in Table 2.

Future perspectives and concluding remarks

Haloalkaliphilic microorganisms, particularly *Bacillus* sp., offer a multitude of actual or potential applications in various fields of biotechnology. Not only do many of them produce compounds of industrial interest, but they also possess useful physiological properties; this can facilitate their exploitation for commercial purposes. Thus, microbial communities in natural haloalkaliphilic environments have attracted attention for

Table 2 Different *Bacillus* sp. in biodegradation and bioremediation studies of environmental pollutants

Bacillus species	Biodegradation and/or Bioremediation of	Effective conditions	Reference
<i>B. subtilis</i> ETL-221	Azo dye decolourisation (crystal violet)	pH 8.0, 40 ° C	Shah et al. (2013a, b, c)
<i>Bacillus</i> sp. VUS	Brilliant blue G	pH 9.0, 50 ° C	Jadhav et al. (2008)
<i>Bacillus</i> sp.	Razomol balck B		Shah et al. (2013a, b, c)
<i>Bacillus</i> sp.	Brown 3 REL		Dawkar et al. (2008)
<i>Bacillus fusiformis</i>	Disperse Blue 79 and Acid Orange 10		Kolekar et al. (2008)
<i>Bacillus cereus</i>	Cibacron black PSG and Cibacron red P4B		Ola et al. (2010)
<i>B. stearothermophilus</i>	Phenol		Gurujeyalakshmi and Oriel (1989)
<i>Bacillus</i> sp., <i>Bacillus brevis</i>	Phenol		Arutchelvan et al. (2006)
<i>Bacillus</i> sp.	polycyclic aromatic hydrocarbons (PAH)	pH 7.0, 60–70 ° C	Feitkenhauer et al. (2003)
<i>B. subtilis</i> , <i>B. cereus</i> , <i>Bacillus cereus</i> , <i>Bacillus sphaericus</i> , <i>B. fusiformis</i> , and <i>B. pumilus</i>	Diesel oil		Bento et al. (2005)
<i>Bacillus</i> sp.,	Hydrocarbons		Ghazali et al. (2004)
<i>Bacillus species</i>	Phenanthrene		Doddamani and Ninnekar (2000)
<i>Bacillus species</i>	Polycyclic aromatic hydrocarbons and long chain alkanes	60–70 ° C	Feitkenhauer et al. (2003)
<i>B. subtilis</i> , <i>B. licheniformis</i> , <i>Bacillus</i> sp,	Heavy Metals		Volesky and Holan (1995)
<i>B. subtilis</i>	Cadmium		Boyanov et al. (2003)
<i>B. subtilis</i>	Lead		Singh et al. (2012)
<i>Bacillus licheniformis</i>	Chromium		Zhou et al. (2007)
<i>Bacillus sphaericus</i> and <i>B. thuringiensis</i>	Cadmium		Allievi and Mariano (2011)
<i>Bacillus marisflavi</i>	Chromium		Mishra and Doble (2008)
<i>Bacillus</i> sp,	Manganese		Hasan et al. (2012)
<i>Bacillus cereus</i>	Arsenic		Giri et al. (2011)
<i>Bacillus</i> sp.	Mercury		Green-Ruiz (2006)
<i>Bacillus subtilis</i>	Mercury		Wang et al. (2010)
<i>Bacillus</i> sp,	Lead and Copper		Tunali et al. (2006)
<i>Bacillus cereus</i>	Arsenic		Giri et al. (2013)
<i>Bacillus subtilis</i>	Arsenic		Yang et al. (2012)

their possible biotechnological use of enzymes, metabolites, and metabolic processes.

Acknowledgments Authors are thankful to Sri Venkateswara University, Tirupati, India for their support and encouragement.

Compliance with ethical standards

Disclosure of potential conflicts of interest All the authors declared that there is no conflict of interest regarding this manuscript and we have not involved any Humans and Animal participants in this manuscript.

Informed consent “Informed consent was obtained from all individual participants included in the study.”

References

- Abbas M, Parveen Z, Iqbal M, Riazuddin IS, Ahmed M, Bhutto R (2010) Monitoring of toxic metals (cadmium, lead, arsenic and mercury) in vegetables of Sindh, Pakistan. *Kathmandu Univ J Sci Eng Technol* 6:60–65
- Adams MWW, Perler FB, Kelly RM (1995) Extremozymes: expanding the limits of biocatalysis. *Biotechnology* 13:662–668
- Ahluwalia SS, Goyal D (2007) Microbial and plant derived biomass for removal of heavy metals from wastewater. *Bioresour technol* 98(12):2243–2257
- Allievi MC, Mariano PA (2011) Metal biosorption by surface-layer proteins from *Bacillus* species. *J Microbiol Biotechnol* 21(2):147–153
- Al-Wahaibi Y, Joshi S, Al-Bahry S, Elshafie A, Al-Bemani A, Shibulal B (2014) Biosurfactant production by ‘*Bacillus subtilis*’ B30 and its application in enhancing oil recovery. *Colloids Surf B: Biointerfaces* 114:324–333
- Annamalai N, Rajeswari MV, Sahu SK, Balasubramanian T (2014) Purification and characterization of solvent stable, alkaline protease from ‘*Bacillus firmus*’ CAS 7 by microbial conversion of marine wastes and molecular mechanism underlying solvent stability. *Proc Biochem* 49(6):1012–1019
- Aono R, Horikoshi K (1991) Carotenes produced by alkaliphilic yellow pigmented strains of *Bacillus*. *Agric Biol Chem* 55:2643–2645
- Ara K, Manabe K, Liu S, Kageyama Y, Ozawa T, Tohata M, Ogasawara N et al (2014) Creation of novel technologies for extracellular protein production toward the development of *Bacillus subtilis* genome factories. In: Anazawa H and Shimizu S (eds) *Microbial production*. Springer Japan. https://books.google.co.in/books/about/Microbial_Production.html?id=s3bpngEACAAJ&redir_esc=y
- Arutchelvan V, Kanakasabai V, Elangovan R, Nagarajan S, Muralikrishnan V (2006) Kinetics of high strength phenol degradation using *Bacillus brevis*. *J Hazard Mater* 129(1):216–222
- Asha BM, Revathi M, Yadav A, Sakthivel N (2012) Purification and characterization of a thermophilic cellulase from a novel cellulolytic strain, *Paenibacillus barcinonensis*. *J Microbiol Biotechnol* 22: 1501–1509
- Atlas RM (1981) Microbial degradation of petroleum hydrocarbons: an environmental perspective. *Microbiol Rev* 45(1):180–209
- Bai J, Yang X, Du R, Chen Y, Wang S, Qiu R (2014) Biosorption mechanisms involved in immobilization of soil Pb by ‘*Bacillus subtilis*’ DBM in a multi-metal-contaminated soil. *J Environ Sci* 26(10): 2056–2064
- Bajaj BK, Singh S, Khullar M, Singh K, Bhardwaj S (2014) Optimization of fibrinolytic protease production from *Bacillus subtilis* I-2 using agro-residues. *Braz Arch Biol Technol* 57(5):653–662
- Barros FFC, Ponezi AN, Pastore GM (2008) Production of biosurfactant by *Bacillus subtilis* LB5a on a pilot scale using cassava wastewater as substrate. *J Ind Microbiol Biotechnol* 35(9):1071–1078
- Bento FM, de Oliveira Camargo FA, Okeke BC, Frankenberger WT (2005) Diversity of biosurfactant producing microorganisms isolated from soils contaminated with diesel oil. *Microbiol Res* 160(3): 249–255
- Boyanov MI, Kelly SD, Kemner KM, Bunker BA, Fein JB, Fowle DA (2003) Adsorption of cadmium to *Bacillus subtilis* bacterial cell walls: a pH-dependent X-ray absorption fine structure spectroscopy study. *Geochim Cosmochim Acta* 67(18):3299–3311
- Caton TM, Witte LR, Ngyuen HD, Buchheim JA, Buchheim MA, Schneegurt MA (2004) Halotolerant aerobic heterotrophic bacteria from the Great Salt Plains of Oklahoma. *Microb Ecol* 48:449–462
- Chandankere R, Yao J, Cai M, Masakorala K, Jain AK, Choi MM (2014) Properties and characterization of biosurfactant in crude oil biodegradation by bacterium ‘*Bacillus methylotrophicus* USTBa’. *Fuel* 122:140–148
- Colwell RR (1977) Ecological aspects of microbial degradation of petroleum in the marine environment. *Crit Rev Microbiol* 5:423–445
- Comte S, Guibaud G, Baudu M (2006) Biosorption properties of extracellular polymeric substances (EPS) resulting from activated sludge according to their type: soluble or bound. *Process Biochem* 41(4): 815–823
- Cui RY, Zheng J, Wu CD, Zhou RQ (2015) Effect of different halophilic microbial fermentation patterns on the volatile compound profiles and sensory properties of soy sauce moromi. *Eur Food Res Technol* 240(3):669–670
- Das K, Mukherjee AK (2007) Comparison of lipopeptide biosurfactants production by *Bacillus subtilis* strains in submerged and solid state fermentation systems using a cheap carbon source: some industrial applications of biosurfactants. *Process Biochem* 42(8):1191–1199
- Das PK, Das S, Sahoo D, Dalei J, Rao VM, Nayak S, Palo S (2014) Comparative evaluation of purification methods for production of polypeptide antibiotics—“Polymyxin B” and “Cerexin A” from *Bacillus* sp. *Pharma Tutor* 2(8):188–200
- Dawkar VV, Jadhav UU, Jadhav SU, Govindwar SP (2008) Biodegradation of disperse textile dye Brown 3REL by newly isolated *Bacillus* sp. VUS. *J Appl Microbiol* 105(1):14–24
- Doddamani HP, Ninnekar HZ (2000) Biodegradation of phenanthrene by a *Bacillus* species. *Curr Microbiol* 41(1):11–14
- Donio MBS, Ronica SFA, Viji VT, Velmurugan S, Jenifer JA, Michaelbabu M, Citarasu T (2013) Isolation and characterization of halophilic *Bacillus* sp. BS3 able to produce pharmacologically important biosurfactants. *Asian Pac J Trop Med* 6(11):876–883
- Esteban-Torres M, Mancheño JM, de las Rivas B, Muñoz R (2015) Characterization of a halotolerant lipase from the lactic acid bacteria ‘*Lactobacillus plantarum*’ useful in food fermentations. *LWT-Food Sci Technol* 60(1):246–252
- Fang Y, Sun X, Yang W, Ma N, Xin Z, Fu J, Hu Q (2014) Concentrations and health risks of lead, cadmium, arsenic, and mercury in rice and edible mushrooms in China. *Food Chem* 147:147–151
- Fatpure BZ (2014) Recent studies in microbial degradation of petroleum hydrocarbons in hypersaline environments. *Front Microbiol* 5: 1–16
- Feitkenhauer H, Müller R, MAuml H (2003) Degradation of polycyclic aromatic hydrocarbons and long chain alkanes at 6070 C by *Thermus* and *Bacillus* spp. *Biodegradation* 14(6):367–372
- Fergus GP (1977) Extracellular enzyme synthesis in the genus *Bacillus*. *Bacteriol Rev* 41:711–753
- Fuchs SW, Jaskolla TW, Bochmann S, Kötter P, Wichelhaus T, Karas M, Entian KD (2011) Entianin, a novel subtilin-like lantibiotic from

- Bacillus subtilis* sub sp. spizizenii DSM 15029T with high antimicrobial activity. Appl Environ Microbiol 77(5):1698–1707
- Garabito MJ, Marquez MC, Ventosa A (1998) Halotolerant *Bacillus* diversity in hypersaline environments. Can J Microbiol 44:95–102
- Gascoyne DJ, Connor JA, Bull AT (1991) Capacity of siderophore-producing alkaliphilic bacteria to accumulate iron, gallium and aluminum. Appl Microbiol Biotechnol 36:136–141
- Ghazali FM, Rahman RNZA, Salleh AB, Basri M (2004) Biodegradation of hydrocarbons in soil by microbial consortium. Int Biodeterior Biodegrad 54(1):61–67
- Giri AK, Patel RK, Mahapatra SS (2011) Artificial neural network (ANN) approach for modelling of arsenic (III) biosorption from aqueous solution by living cells of *Bacillus cereus* biomass. Chem Eng J 178:15–25
- Giri AK, Patel RK, Mahapatra SS, Mishra PC (2013) Biosorption of arsenic (III) from aqueous solution by living cells of *Bacillus cereus*. Environ Sci Pollut Res 20(3):1281–1291
- Gong R, Ding Y, Yang C, Liu H, Sun Y (2005) Dyes Pigment 64:187–192
- Goyer RA, Chisholm JJ (1972) Lead. In: Lee DHK (ed) Metallic contaminants in human health, London Academy Press, pp 57–95
- Grant WD (2006) Alkaline environments and biodiversity. *Extremophiles*. UNESCO, Eolss Publishers, Oxford
- Green-Ruiz C (2006) Mercury (II) removal from aqueous solutions by nonviable *Bacillus* sp. from a tropical estuary. Bioresour Technol 97(15):1907–1911
- Gurujeyalakshmi G, Oriol P (1989) Isolation of phenol-degrading *B. stearothermophilus* and partial characterization of the phenol hydroxylase. Appl Environ Microbiol 55(2):500–502
- Gutnick DL, Bach H (2000) Engineering bacterial biopolymers for the biosorption of heavy metals; new products and novel formulations. Appl Microbiol Biotechnol 54:451–460
- Hamasaki N, Shirai S, Niitsu M, Kakinuma K, Oshima T (1993) An alkaliphilic *Bacillus* sp. produces 2-phenylethylamine. Appl Environ Microbiol 59:2720–2722
- Harayama S, Kasai Y, Hara A (2004) Microbial communities in oil-contaminated seawater. Curr Opin Biotechnol 15:205–214
- Hasan HA, Abdullah SRS, Kofli NT, Kamarudin SK (2012) Isotherm equilibria of Mn 2+ biosorption in drinking water treatment by locally isolated *Bacillus* species and sewage activated sludge. J Environ Manag 111:34–43
- Hassen A, Saidi N, Cherif M, Boudabous A (1998) Resistance of environmental bacteria to heavy metal. Bioresour Technol 64:7–15
- Head IM, Jones DM, Roling WF (2006) Marine microorganisms make a meal of oil. Nat Rev Microbiol 4:173–182
- Hezayen FF, Rehm BHA, 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
- Hinteregger C, Streichsberg F (1997) *Halomonas* sp. a moderately halophilic strain, for biotreatment of saline phenolic waste-water. Biotechnol Lett 19(11):1099–1102
- Horikoshi K (1996) Alkaliphiles from an industrial point of view. FEMS Microbiol Rev 18:259–270
- Horikoshi K (1999) Alkaliphiles: some applications of their products for biotechnology. Microbiol Mol Biol Rev 63(4):735–750
- Horikoshi K (2011) General physiology of alkaliphiles. In: Extremophiles handbook, Springer, pp 100–119. doi: 10.1007/978-4-431-53898-1_2.5
- Ibrahim ASS, El-diwany AI (2007) Isolation and identification of new cellulase producing thermophilic bacteria from an Egyptian hot spring and some properties of the crude enzyme. Aust J Basic Appl Sci 1:473–478
- Imhoff JF, Sahl HG, Soliman GSH, Trüper HG (1979) The Wadi Natrun chemical composition and microbial mass developments in alkaline brines of eutrophic desert lakes. Geomicrobiol J 1:219–234
- Jadhav SU, Jadhav MU, Kagalka AN, Govindwar SP (2008) Decolorization of Brilliant Blue G dye mediated by degradation of the microbial consortium of *Galactomyces geotrichum* and *Bacillus* sp. J Chin Inst Chem Eng 39(6):563–570
- Jenneman GE, McInemey MJ, Knapp RM, Clark JB, Feero JM, Revus DE, Menzie DE (1983) Halotolerant, biosurfactant-producing *Bacillus* species potentially useful for enhanced oil recovery. Dev Ind Microbiol 24:485–492
- Jones BE, Grant WD, Collins NC, Mwatha WC (1994) Alkaliphiles: diversity and identification. In: Priest FG, Ramos-Cormenzana A, Tindall BJ (eds) Bacterial diversity and systematics. Plenum Press, New York, pp 195–230
- Joshi S, Yadav S, Nerurkar A, Desai AJ (2007) Statistical optimization of medium components for the production of biosurfactant by *Bacillus licheniformis* K51. J Microbiol Biotechnol 17(2):313
- Joshi SJ, Suthar H, Yadav AK, Hingurao K, Nerurkar A (2012) Occurrence of biosurfactant producing *Bacillus* sp. in diverse habitats. ISRN biotechnology. doi:10.5402/2013/652340
- Kamekura M, Onishi H (1974) Halophilic nuclease from a moderately halophilic *Micrococcus varians*. J Bacteriol 119:339–344
- Kolekar YM, Pawar SP, Gawai KR, Lokhande PD, Shouche YS, Kodam KM (2008) Decolorization and degradation of Disperse Blue 79 and Acid Orange 10, by *Bacillus fusiformis* KMK5 isolated from the textile dye contaminated soil. Bioresour Technol 99(18):8999–9003
- Koller M, Bona R, BrauneGG G, Hermann C, Horvat P, Kroutil M, Varila P (2005) Production of polyhydroxyalkanoates from agricultural waste and surplus materials. Biomacromolecules 6(2):561–565
- Kratochvil D, Volesky B (1998) Advances in the biosorption of heavy metals. Trends Biotechnol 16(7):291–300
- Krulwich TA, Liu J, Morino M, Fujisawa M, Masahiro Ito M, Hicks DB (2011) Adaptive mechanisms of extreme alkaliphiles. In: Horikoshi K (ed) Extremophiles handbook. Springer, pp 120–140 doi: 10.1007/978-4-431-53898-1_2.6
- Kulichevskaya IS, Milekhina EI, Borzenkov IA, Zvyagintseva IS, Belyaev SS (1992) Oxidation of petroleum hydrocarbons by extremely halophilic *archaeobacteria*. Microbiology 60:596–601
- Kumar T, Singh M, Purohit HJ, Kalia VC (2009) Potential of *Bacillus* sp. to produce polyhydroxybutyrate from biowaste. J Appl Microbiol 106(6):2017–2023
- Lanyi JK (1993) Proton translocation mechanism and energetics in the light-driven pump bacteriorhodopsin. Biochim Biophys Acta (BBA) Bioenerg 1183(2):241–261
- Liu H, Fang HH (2002) Characterization of electrostatic binding sites of extracellular polymers by linear programming analysis of titration data. Biotechnol Bioeng 80(7):806–811
- Liu J, Wu H, Feng J, Li Z, Lin G (2014) Heavy metal contamination and ecological risk assessments in the sediments and zoobenthos of selected mangrove ecosystems, South China. Catena 119:136–142
- Ma Y, Zhang W, Xue Y, Zhou P, Ventosa A, Grant WD (2004) Bacterial diversity of the Inner Mongolian Baer Soda Lake as revealed by 16S rRNA gene sequence analysis. Extremophiles 8:45–51
- Mansour SA (2014) Monitoring and health risk assessment of heavy metal contamination in food. Practical food safety: contemporary issues and future directions. p. 235–255. doi:10.1002/9781118474563.ch13
- Marco P, Erhard B (2011) Cellular adjustments of *Bacillus subtilis* and other bacilli to fluctuating salinities. In: Antanio O, Aharon O, Yanhe M (eds) halophiles and hypersaline environments. doi: 10.1007/978-3-642-20198-1
- Margesin R, Schinner F (2001) Biodegradation and bioremediation of hydrocarbons in extreme environments. Appl Microbiol Biotechnol 56:650–663
- Martinez DST, Faria AF, Berni E, Souza Filho AG, Almeida G, Caloto-Oliveira A, Alves OL (2014) Exploring the use of biosurfactants from *Bacillus subtilis* in bionanotechnology: a potential dispersing

- agent for carbon nanotube ecotoxicological studies. *Process Biochem* 49(7):1162–1168
- Marvasi M, Visscher PT, Martinez LC (2010) Exopolymeric substances (EPS) from *Bacillus subtilis*: polymers and genes encoding their synthesis. *FEMS Microbiol Lett* 313(1):1–9
- Maugeri TL, Gugliandolo C, Caccamo D, Panico A, Lama L, Gambacorta A, Nicolaus B (2002) A halophilic thermotolerant *Bacillus* isolated from a marine hot spring able to produce a new exopolysaccharide. *Biotechnol Lett* 24(7):515–519
- Maulin PS, Patel KA, Nair SS, Darji AM (2014) An application of response surface methodology in microbial degradation of Azo Dye by *Bacillus subtilis* ETL-1979. *Am J Microbiol Res* 2(1):24–34
- Meyer H, Weidmann H, Mäder U, Hecker M, Völker U, Lalk M (2014) A time resolved metabolomics study: the influence of different carbon sources during growth and starvation of *Bacillus subtilis*. *Mol Biosyst* 10(7):1812–1823
- Mishra S, Doble M (2008) Novel chromium tolerant microorganisms: isolation, characterization and their biosorption capacity. *Ecotoxicol Environ Saf* 71(3):874–879
- Morikawa M (2006) Beneficial biofilm formation by industrial bacteria *Bacillus subtilis* and related species. *J Biosci Bioeng* 101(1):1–8
- Mosin O, Ignatov I (2014) Photochrome transmembrane protein bacteriorhodopsin from purple membranes of *Halobacterium Halobium* in nano- and biotechnologies. *J Med Physiol Biophys* 4:81–99
- Mukherjee AK, Das K (2005) Correlation between diverse cyclic lipopeptides production and regulation of growth and substrate utilization by *Bacillus subtilis* strains in a particular habitat. *FEMS Microbiol Ecol* 54(3):479–489
- Müller V, Köcher S (2011) Adapting to changing salinities: biochemistry, genetics, and regulation in the moderately halophilic bacterium *Halobacillus halophilus*. In: Horikoshi K (ed) *Extremophiles Handbook*. Springer, Tokyo, pp 383–400
- Mullen MD, Wolf DC, Ferris FC, Beveridge TJ, Flemming CA, Bailey FW (1989) Bacterial sorption of heavy metals. *Environ Microbiol* 55:3143–3149
- Nieto JJ, Fernandez-Castillo R, Marquez M, Ventosa A, Quesada E, Ruiz-Berraquero F (1989) Survey of metal tolerance in moderately Halophilic eubacteria. *Appl Environ Microbiol* 55:2385–2390
- Nriagu JO (1988) A silent epidemic of environmental metal poisoning. *Environ Pollut* 50:139–161
- Ola IO, Akintokun AK, Akpan I, Omomowo IO, Areo VO (2010) Aerobic decolourization of two reactive azo dyes under varying carbon and nitrogen source by *Bacillus cereus*. *Afr J Biotechnol* 9(5):672–677
- Ongena M, Jacques P (2008) *Bacillus* lipopeptides: versatile weapons for plant disease biocontrol. *Trends Microbiol* 16(3):115–125
- Oren A (2002a) Properties of halophiles. In: *Halophilic microorganisms and their environments*. Springer, pp 233–278. <http://www.springer.com/us/book/9781402008290>
- Oren A (2002b) Halophilic microorganisms and their environments In: cellular origin and life in extreme habitats. <http://www.springer.com/us/book/9781402008290>
- Oren A (2006) Life at high salt concentrations. In: Dworkin M, Falkow S, Rosenberg E, Schleifer KH, Stackebrandt E (eds) *The prokaryotes. A handbook on the biology of bacteria: ecophysiology and biochemistry*, vol 2. Springer, New York, pp 263–282
- Paavilainen S, Helisto P, Korpela T (1994) Conversion of carbohydrates to organic acids by alkaliphilic bacilli. *J Ferment Bioeng* 78:217–222
- Padamavathy S, Sandhya S, Swaminathan K, Subrahmanyam YV, Kaul SN (2003) Comparison of decolourization of reactive azo dyes by microorganisms isolated from various source. *J Environ Sci* 15:628–632
- Patel R, Dodia M, Singh SP (2005) Extracellular alkaline protease from a newly isolated haloalkaliphilic *Bacillus* sp.: Production and optimization. *Process Biochem* 40(11):3569–3575
- Pearce CI, Lloyd JR, Guthrie JT (2003) The removal of colour from textile wastewater using whole bacterial cells: a review. *Dyes Pigments* 58:179–196
- Pedros-Alió C (2006) Marine microbial diversity: can it be determined? *Trends Microbiol* 14(6):257–263
- Peyton B, Wilson M, Tomás Y, David R (2002) Kinetics of phenol biodegradation in high salt solutions. *Water Res* 36:4811–4820
- Pirri G, Giuliani A, Nicoletto SF, Pizzuto L, Rinaldi AC (2009) Lipopeptides as anti-infectives: a practical perspective. *Cent Eur Journal Biol* 4(3):258–273
- Prakash N, Gopal S (2014) Analysis of the glycoside hydrolase family 8 catalytic core in cellulase-chitosanases from *Bacillus* sp. *Int J Comput Bioinfo ISilico Model* 3(1):315–320
- Price NP, Rooney AP, Swezey JL, Perry E, Cohan FM (2007) Mass spectrometric analysis of lipopeptides from *Bacillus* strains isolated from diverse geographical locations. *FEMS Microbiol Lett* 271(1): 83–89
- Priest FG (1977) Extracellular enzyme synthesis in the Genus *Bacillus*. *Bacteriol rev. Am Soc Microbiol* 41(3):711–753
- Purohit MK, Raval VH, Singh SP (2014) Haloalkaliphilic bacteria: molecular diversity and biotechnological applications. In: *Geomicrobiology and biogeochemistry*. Springer Berlin Heidelberg, pp 61–79
- Quesada E, Ventosa A, Rodriguez VF, Megias L, Ramos CA (1983) Numerical taxonomy of moderately halophilic Gram-negative bacteria from hypersaline soils. *J Gen Microbiol* 129:2649–2657
- Quillaguamán J, Guzmán H, Van-Thuoc D, Hatti-Kaul R (2010) Synthesis and production of polyhydroxyalkanoates by halophiles: current potential and future prospects. *Appl Microbiol Biotechnol* 85(6):1687–1696
- Raaijmakers JM, De Bruijn I, Nybroe O, Ongena M (2010) Natural functions of lipopeptides from *Bacillus* and *Pseudomonas*: more than surfactants and antibiotics. *FEMS Microbiol Rev* 34(6):1037–1062
- Raliya R, Tarafdar JC, Mahawar H, Kumar R, Gupta P, Mathur T, Gehlot HS (2014) ZnO nanoparticles induced exopolysaccharide production by *B. subtilis* strain JCT1 for arid soil applications. *Int J Biol Macromol* 65:362–368
- Rani G, Prema A, Seema K, Saxena RK, Mohapatra H (2000) Microbial biosorbents: meeting challenges of heavy metal pollution in aqueous solutions. *Curr Sci* 78(8):967–973
- Rothschild LJ, Mancinelli RL (2001) Life in extreme environments. *Nature* 409:1092–1101
- Rudd T, Sterritt RM, Lester JN (1984) Complexation of heavy metals by extracellular polymers in the activated sludge process. *J Water Pollut Control Fed* 12(56):1260–1268
- Sabina K, Fayidh MA, Archana G, Sivarajan M, Babuskin S, Babu PAS, Sukumar M (2014) Microbial desalination cell for enhanced biodegradation of waste engine oil using a novel bacterial strain *Bacillus subtilis* moh3. *Environ Technol* 35(17):2194–2203
- Saju KA, Michael BM, Murugan M, Thiravias RS (2011) Survey on Halophilic microbial diversity of Kovalam Salt pans in Kanyakumari District and its industrial applications. *J Appl Pharm Sci* 01(05):160–163
- Salehizadeh H, Shojaosadati SA (2003) Removal of metal ions from aqueous solution by polysaccharide produced from *Bacillus firmus*. *Water Res* 37:4231–4235
- Santimano MC, Prabhu NN, Garg S (2009) PHA production using Low-cost agro-industrial wastes by *Bacillus* sp. Strain COLI/Afi. *Res J Microbiol* 4(3):89–96
- Sarafin Y, Donio MBS, Velmurugan S, Michaelbabu M, Citarasu T (2014) *Kocuria marina* BS-15 a biosurfactant producing halophilic bacteria isolated from solar salt works in India. *Saudi J Biol Sci* 21(6):511–519
- Sass AM, McKew BA, Sass H, Fichtel J, Timmis KN, McGenity TJ (2008) Diversity of *Bacillus*-like organisms from deep-sea hypersaline anoxic sediments. *Saline Syst* 4:8

- Schiraldi C, De Rosa M (2002) The production of biocatalysts and biomolecules from extremophiles. *TRENDS Biotechnol* 20(12):515–521
- Shah MP, Patel KA, Nair SS (2013a) Microbiological removal of crystal violet dye by *Bacillus subtilis* ETL-2211. *OA Biotechnol* 2(1):9
- Shah MP, Patel KA, Nair SS, Darji AM (2013b) Microbial degradation of Textile Dye (Remazol Black B) by *Bacillus* spp. *ETL-2012*. *J Bioremed Biodeg* 4(180):2
- Shah MP, Patel KA, Nair SS, Darji AM (2013c) Potential effect of Two *Bacillus* sp. on decolorization of Azo dye. *J Bioremed Biodeg* 4:199
- Shindo K, Misawa N (2014) New and rare carotenoids isolated from marine bacteria and their antioxidant activities. *Mar Drugs* 12(3):1690–1698
- Shyamala GR, Vijayaraghavan R, Meenambigai P (2014) Microbial degradation of reactive dyes—A review. *Int J Curr Microbiol App Sci* 3(3):421–436
- Simpson DR, Natraj NR, McInerney MJ, Duncan KE (2011) Biosurfactant-producing *Bacillus* are present in produced brines from Oklahoma oil reservoirs with a wide range of salinities. *Appl Microbiol Biotechnol* 91(4):1083–1093
- Singh S, Bajaj BK (2014) Medium optimization for enhanced production of protease with industrially desirable attributes from *Bacillus subtilis* K-1. *Chem Eng Commun* 202(8):1051–1060
- Singh U, Singh BP, Singh KK (2012) Lead removal from aqueous solutions by *Bacillus subtilis*. *J Chem Pharm Res* 4(4):2242–2249
- Smith FB (1938) An investigation of a taint in the rib bones of bacon. The determination of halophilic Vibrios. *Proc R Soc Queensland* 49:29–52
- Souayah M, Al-Waheibi YM, Al-Bahry S, Elshafie A, Al-Bemani A, Joshi S, Al-Mandhari M (2014) Optimization of low concentration *Bacillus subtilis* strain biosurfactant towards microbial enhanced oil recovery. *Energy Fuels* 28(9):5606–5611
- Swannell RP (1999) Bioremediation of petroleum hydrocarbon contaminants in marine habitats. *Curr Opin Biotechnol* 10:234–239
- Syed S, Paramageetham CH (2015) Heavy metal detoxification by different *Bacillus* species isolated from solar salterns. *Scientifica* Article ID 319760. doi:10.1155/2015/319760
- Syed S, Prasada BG, Paramageetham CH (2012) A Measure of Soil microbial diversity and density from Artificial Solar Salterns in Nellore District in A.P, INDIA. *Int J Res Biol Sci* 2(2):83–86
- Syed S, Prasada BG, Paramageetham CH (2013a) Isolation of amylase producing bacteria from solar salterns of Nellore district Andhra Pradesh, India. *Res Rev J Microbiol* 2(1):1
- Syed S, Prasada BG, Paramageetham CH (2013b) Extracellular enzymatic potential of haloalkaliphiles from solar salterns of Nellore district A.P. India. *Asian J Biol Sci* 4(2):302–305
- Tambekar DH, Dhundale VR (2012) Studies on the physiological and cultural diversity of *Bacilli* characterized from Lonar lake (Ms) India. *Biosci Discov* 3(1):34–39
- Tunali S, Cabuk A, Akar T (2006) Removal of lead and copper ions from aqueous solutions by bacterial strain isolated from soil. *Chem Eng J* 115(3):203–211
- Ventosa A, Quesada E, Rodri'guez-Valera F, Ruiz-Berraquero F, Ramos-Cornenzana A (1998) Numerical taxonomy of moderately halophilic Gram-negative rods. *J Gen Microbiol* 128:1959–1968
- Verlinden RA, Hill DJ, Kenward MA, Williams CD, Radecka I (2007) Bacterial synthesis of biodegradable polyhydroxyalkanoates. *J Appl Microbiol* 102(6):1437–1449
- Vijayaraghavan K, Yun YS (2008) Biosorption of C.I. Reactive Black 5 from aqueous solution using acid treated biomass of brown seaweed *Laminaria* sp. *Dyes Pigment* 76:726–732
- Volesky B, Holan ZR (1995) Biosorption of heavy metals. *Biotechnol Prog* 11:235–250
- Wang XS, Li FY, He W, Miao HH (2010) Hg (II) removal from aqueous solutions by *Bacillus subtilis* biomass. *Clean-Soil Air Water* 38(1):44–48
- Wingender J, Neu TR, Flemming HC (1999) What are bacterial extracellular polymeric substances? In: *Microbial extracellular polymeric substances*. Springer, Berlin Heidelberg, pp 1–19
- Wong PK, Yuen PY (1996) Decolourisation and biodegradation of methyl red by *Klebsiella pneumoniae* RS-13. *Water Res* 30:1736–1744
- Wongsasuluk P, Chotpanarat S, Siri Wong W, Robson M (2014) Heavy metal contamination and human health risk assessment in drinking water from shallow groundwater wells in an agricultural area in Ubon Ratchathani province, Thailand. *Environ Geochem Health* 36(1):169–182
- Woolard CR, Irvine RL (1994) Biological treatment of hypersaline wastewater by a biofilm of halophilic bacteria. *Water Environ Res* 66:230–235
- Wu L, Wu H, Chen L, Xie S, Zang H, Borriss R, Gao X (2014) Bacilysin from *Bacillus amyloliquefaciens* FZB42 has specific bactericidal activity against harmful algal bloom species. *Appl Environ Microbiol*. AEM-02605
- Xu XW, Wu YH, Zhou Z, Wang CS, Zhou YG, Zhang HB, Wu M (2007) *Halomonas saccharevitans* sp. nov., *Halomonas arcis* sp. nov. and *Halomonas subterranea* sp. nov., halophilic bacteria isolated from hypersaline environments of China. *Int J Syst Evol Microbiol* 57(7):1619–1624
- Yang T, Chen ML, Liu LH, Wang JH, Dasgupta PK (2012) Iron (III) modification of *Bacillus subtilis* membranes provides record sorption capacity for arsenic and endows unusual selectivity for As (V). *Environ Sci Technol* 46(4):2251–2256
- Yilmaz M, Soran H, Beyatli Y (2005) Determination of poly- β -hydroxybutyrate (PHB) production by some *Bacillus* spp. *World J Microbiol Biotechnol* 21(4):565–566
- Yuan J, Li B, Zhang N, Waseem R, Shen Q, Huang Q (2012) Production of bacillomycin-and macrolactin-type antibiotics by *Bacillus amyloliquefaciens* NJN-6 for suppressing soilborne plant pathogens. *J Agric Food Chem* 60(12):2976–2981
- Zhang W, Angelini T, Tsai SM, Nixon R (2014) EPS forces in *Bacillus subtilis* biofilms. *Bullet Am Phys Soc* :59
- Zhou M, Liu Y, Zeng G, Li X, Xu W, Fan T (2007) Kinetic and equilibrium studies of Cr (VI) biosorption by dead *Bacillus licheniformis* biomass. *World J Microbiol Biotechnol* 23(1):43–48
- Zhu Z, Zhang G, Luo Y, Ran W, Shen Q (2012) Production of lipopeptides by *Bacillus amyloliquefaciens* XZ-173 in solid state fermentation using soybean flour and rice straw as the substrate. *Bioresour Technol* 112:254–260
- Zvyagintseva IS, Poglasova MN, Gotoeva MT, Belyaev SS (2001) Effect of the medium salinity on oil degradation by nocardio form bacteria. *Microbiology* 70:652–656