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Review

Hypersaline habitats and halophilic microorganisms

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Abstract: Hypersaline habitats are present all over the globe in the form of saline soil, saline water and salted food. Some of the more famous hypersaline habitats are the Dead Sea (Jordan-Israel), the Great Salt Lake (USA), the Solar Lake and lakes at Natrun valley (Egypt), and the inland saltern of La Mala (Spain). Halophilic microorganisms can be classified into halophilic algae, bacteria and fungi, while the halophilic bacteria are further classified into extremely halophilic bacteria, moderately halophilic bacteria, moderately halophilic eubacteria and moderately halophilic archaeobacteria. Two kinds of mechanisms, known as 'salt in' and 'low salt in', are typically exhibited by halophilic microorganisms in their adaptation to high salt concentrations. Several reports have suggested that halophilic microorganisms can be polyextremophilic. Evaluating the physiology of halophilic microorganisms and their adaptation to the environment allows a better understanding of the extremophilic characteristics of the microorganisms. Halophiles have been used in a number of biotechnological applications, making them an interesting and important choice of research topic in this era of biotechnology. This review is an attempt to give a basic understanding of halophilic microorganisms, their habitats, adaptation, as well as their importance in the current biotechnological developments.

Keywords: extreme habitats, hypersaline environments, extremophiles, halophiles

INTRODUCTION

Millions of hectares of land around the world are saline and more are becoming prone to salinity due to the accumulation of salt, making them increasingly unsuitable for agriculture [1], with an estimated ~25% of all irrigated lands currently being covered by saline areas [2]. Thus, there is an increasing need to understand saline environments and the microbial diversity found in these saline systems. As a model system to understand the interactions of simple ecosystems where only few types of microorganisms are found, extremophiles, and in particular halophiles, are of interest especially when considering the future possibility of increasing food shortage and food preservation problems as well as other aspects such as expeditions on Mars [3-5].

Hypersaline environments, also known as thalassohaline environments, mostly resemble those of the salterns and are caused by the evaporation of sea water [6], which leaves behind deposits of minerals, mostly dominated by the presence of sodium chloride (NaCl), to levels of more than 300 Practical Salinity Units (PSU) [6, 7]. The composition of salts and pH of the area mostly resemble that of sea water [8]. Many microorganisms have been reported to inhabit salterns, including algae, bacteria and fungi [9].

A large number of known microorganisms that grow and survive under normal conditions are unable to produce the desired results when applied in biotechnology due to the unfavourable conditions for their survival or for the activity that is required in that operation. Thus, understanding hypersaline environments and the adaptation made by their microbial inhabitants can potentially lead to new biotechnological applications or help find resistance genes that can then be incorporated into food crops or other organisms to allow their optimal growth or their products (such as enzymes) to be used under more extreme conditions (temperature, pressure, pH and salinity) [10].

This review is intended to allow readers from any part of society to understand the basic knowledge of hypersaline environments, their microbial inhabitants, the adaptation to halophilic conditions used by halophilic microbes, the polyextremophilic modes of halophilic microorganisms, and the current and potential biotechnological applications of halophilic microorganisms.

HYPERSALINE HABITATS

Hypersaline habitats can be classified based on the extremity, adaptability and geological and geographical location of the area.

Saline Soil

Soil habitats are heterogeneous and are comprised of a diverse range of minerals and salinity present within the soil at various depths [11]. Soil salinity is much more variable than water salinity [12]. Higher plants that are halotolerant (halophytes) are well adapted to growing in different levels of salinity and play important roles in different ecological nutrient cycles, but the interactions between plants and microbes vary with different saline habitats [13].

A number of bacterial species have been reported to inhabit saline soils, but the dominant species found in such habitats belong to the *Bacillus*, *Pseudomonas*, *Micrococcus* and *Alcaligenes* genera [6]. In the Alicante, Spain, the rhizosphere and hypersaline soil have been reported to contain 5–10% NaCl. The xerophytic plants present in the area and the salt concentration range allowed the growth of isolated organisms that are not related to the salinity of the soil [14]. Half of the plants were able to grow best in a high-salinity condition (5–15% NaCl) while the other half grew best in a low-salinity condition (1% NaCl). With respect to the culturable microbes from this environment, agar media plates with 10% NaCl revealed mostly the presence of Gram-positive rod bacteria, while Gram-negative rod bacteria were found to be abundant at NaCl concentrations of 10–20%. Gram-positive cocci bacteria were found in soil with ≥ 20% NaCl salinity, and were mostly from the *Bacillus*, *Micrococcus*, *Staphylococcus*, *Actinomycetes*, *Corynebacterium*, *Planococcus, Arthrobacter* and *Nocardia* genera [6].

Saline Water

Water with salinity of 3% or above is designated as saline water [15]. Brackish water, sea and oceanic water and water from salt lakes and salterns are all considered as saline water. Some of the more famous soil and saline water habitats are discussed below.

The Dead Sea

The Dead Sea is a typical example of the thalassohaline habitat. It is a lake approximately 320 m in depth with a water temperature of 21–36 ^{o}C and a salt concentration of 78% NaCl. The pH is slightly low and Na^{+}, Cl^{-} and Mg^{2+} are the most abundant ions present [16].

A number of studies have characterised the halophilic microorganisms present in the Dead Sea and those found include the eubacteria, which were aerobes or facultative anaerobes of the genera *Pseudomonas* [17], *Flavobacterium* [17], *Chromobacterium* [17,18], *Halobacterium* [19], *Halococcus* [20], *Clostridium* [21], *Sporohalobacter* [22] and *Halomonas* [23], plus a novel species *Halobaculum gomorrense* [24]. In addition, filamentous halophilic fungi have also been reported recently from the Dead Sea [25], and so it is clear that it does in fact support life despite the high salinity.

The Great Salt Lake, USA

The Great Salt Lake (GSL) is situated in Utah, USA, and is the largest salt lake in the Western hemisphere. This is a thalassohaline lake of moderate depth (~10 m maximum) situated in a salt desert. Unlike the Dead Sea, the GSL has a relatively high pH on the alkaline side, with a high salinity of 33% NaCl [16]. However, the salt concentration has recently changed dramatically due to the activity around the GSL since 1959 [14]. The causeway that has been constructed separates the GSL into three regions (north-east, north-west and south) and prevents the mixing of water, which has resulted in two independent water habitats, the north side and the south side, where the salt concentration of the latter (12% NaCl) is much lower than that of the former (34% NaCl) [16]. The low salinity of the south side is due to a continuous supply of fresh water from the surrounding mountains. The major ions in the lake are Na^{+} and Cl^{-}, and the water temperature of the lake is seasonal, ranging from -5 to 35 ^{o}C [14, 16].

The GSL has a bacterial community which has been classified into three groups. The first is the archaeobacteria and includes members of the *Halococcus* and *Halobacterium* genera that are mostly present in the north side of the GSL due to the extreme salinity. Species like *Halorhabdus utahensis* [26] and *Methanohalophilus muhii* [27] are also found in the GSL. The second is the eubacteria, which can be aerobes or facultative anaerobes and includes *Halomonas variabilis* [28], *Pseudomonas halophila* [28], *Chromohalobacter marismortui* [18], *Halobacillus trueperi* and *Halobacillus litoralis* [29]. Finally, the third group is the anaerobic eubacteria, with *Haloanaerobium praevalens* [30] and *Desulfocella halophila* [31] being commonly found.

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The Solar Lake, Egypt

The Solar Lake, located on the Sinai coast region of the Gulf of Aqaba, is also an extremely hypersaline lake, with a shallow depth of 4–6 m. The solar intensity reaches the bottom of the lake (hence providing the name of the Solar Lake), which has a high rate of evaporation and intense and complex microbial interactions in the sediment as well as in the water [32]. In summer, the water in the lake gets completely oxygenated but in autumn it stratifies. The salinity of the lake rises to 20% NaCl in the summer due to the high rate of evaporation. A gravel bar of 60 m in width separates the lake from the Red Sea. The Lake gets contaminated from the Red Sea and also by occasional showers [16].

The halophilic archaeal community isolated from this lake is dominated by *Halobacteriaceae*, *Methanococcus, Methanobacterium*, *Spirochaeta halophila* and *Desulfovibrio halophiles.* The moderately halophilic bacteria found in the lake include *Beggiatoa alba* and *Achromatium volutans,* a sulphur utilising bacteria [27]. The normal varieties of halophilic bacteria are not present much in the area and the community also changes due to the continuous variation in the saline conditions of the lake.

Lakes at Natrun Valley (Wadi El Natrun), Egypt

The Natrun Valley or Wadi El Natrun is situated below sea level in the arid region of central northern Egypt. The northern region of the valley has eight seasonal hypersaline lakes that are sometimes completely dry. Like the Solar Lake, the lakes at Natrun Valley also have a high rate of evaporation. The water feed is provided from underground seepage of water from the Great Nile River that touches the area through the burdi swamps (grass swamps) [16].

The salinity near the sediment around the valley varies in the range of 3.1–8.6% NaCl. The Gram-positive bacterium *Bacillus haloalkaliphilus*, a polyextremophilic bacterium that shows alkalophilic and halophilic characteristics, has been isolated from these lakes [33]. This bacterium show a maximum growth in 0.5–3 M (~2.9–17.5%) NaCl and can even tolerate 4 M (~23.4%) NaCl. Some other alkalophilic and phototrophic bacteria have also been reported from the Natrun Valley [16].

Inland saltern of La Mala, Spain

The La Mala area is situated 780 m above sea level with a 2% slope [34]. The area is thalassohaline and the salt bed is created from the saline water near the surface of the soil. The other source of water that feeds the habitat is well water. The chloride concentration fed by the well water is lower than the content of Mg^{2+}, Ca^{2+} and K^{+} ions from sea water.

The total salinity found in the well water is 18% NaCl. The main halotolerant species isolated from the La Mala salterns are bacteria, with the major genera being *Alteromonas*, *Flavobacterium*, *Halomonas*, *Acinetobacter*, *Vibrio*, *Halobacterium* and *Pseudomonas* [35].

Salted Food

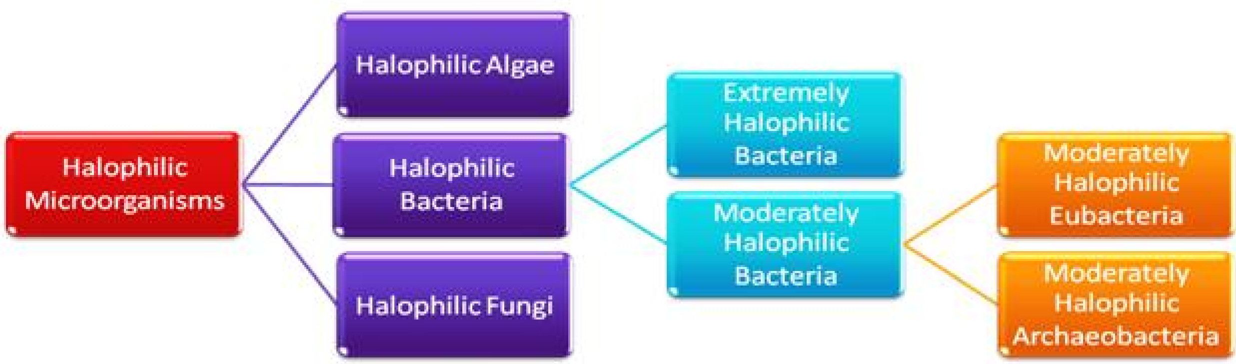
Fungi, especially yeasts, are common contaminants of salted food [3], along with some halophilic bacteria including *Pediococcus halophilus* [36], *Halobacterium* sp. [37], *Halococcus* sp. [37], *Halomonas salina* [38], *Pseudomonas beijerinckii* [27]*, Halomonas halodenitrificans* [27] and *Vibrio costicola* [27]. The spoiling of food when preserved in salt can occur due to the toxins produced from these microorganisms, for example the aflatoxins from members of the *Aspergillus* genus.

HALOPHILIC MICROORGANISMS

Microorganisms that can survive, grow and reproduce in extreme saline conditions are known as halophilic microorganisms or halophiles. They are mostly prokaryotes but include some eukaryotes as well. They have the ability to withstand the denaturing effects of salts as well as to manage and maintain the equilibrium between the high environmental osmotic pressure and the low water activity (w_a) level outside the cell, compared to that within the intracellular (in the case of prokaryotes) or intercellular (in the case of eukaryotes) regions [39]. The halophilic microorganisms that have been most extensively studied are *Aphanothece halophytica* (cyanobacteria), *Halobacterium* spp. (archaea), *Dunaliella salina* (green alga) and *Hortaea werneckii* (fungus) [14].

There is a diverse range of halophilic classifications. According to Kushner [40], halophiles can be categorised into five major classes on the basis of the amount of NaCl they require for their growth. These are (i) non-halophiles, (ii) mild halophiles, (iii) moderate halophiles, (iv) borderline extreme halophiles and (v) extreme halophiles. Non-halophiles grow in < 0.2 M (< 1.2%) NaCl [41] and can be normal microorganisms that only require NaCl as one of their nutrients, or mild halotolerant ones that can tolerate a low salt concentration. Mild halophiles require 0.2–0.5 M (~1.2–2.9%) NaCl and are mostly halotolerant species that can be facultative halophiles. Moderate halophiles require 0.5–2.5 M (~2.9–13.6%) NaCl and represent the emergence of the real halophiles as they require moderate salt concentration for their growth and other metabolic purposes. Borderline extreme halophiles require 1.5–4.0 M (~8.8–23.4%) NaCl and can adapt themselves to withstand the high salt concentrations. Most of them are obligate halophiles. Extreme halophiles require 2.5–5.2 M (~13.6–30.4%) NaCl and are the most modified form of halophiles. Almost all of them are obligate halophiles. Mostly comprised of halophilic archeae [3], microorganisms belonging to this group can be considered as one of the toughest (most specialised) kinds of organisms living on this planet, being able to adapt themselves to growing in high salt concentrations. They are equipped with specialised molecular adjustments, including halozymes that are capable of working at high salt concentration, gas vesicles that provide floating characteristics to the cells and the presence of sensory rhodopsins that promote reactions involving light [6]. These capabilities for adaptation of the extreme halophilic microorganisms make them interesting candidates for biotechnological applications in various processes of large-scale biochemical reactions [4].

As shown in Scheme 1, halophilic microorganisms can be found in all domains of life amongst bacteria, archaea and eukarya.



Scheme 1. Classification of halophiles into major groups of microorganisms

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Halophilic Algae

A few algal species are known to be halophiles and are distributed in the water of salterns, oceans, crystallisation ponds and microbial beds in hypersaline environments, and are facultative rather than obligate halophiles [42]. Halophilic algal species show polyextremophilic behaviour and include species such as *Chlamydomonas nivalis* (a psycrophilic green alga) and *Cyanidium caldarium* (a red thermophilic alga). The most well-known halophilic algal species is the green alga *Dunaniella salina*, which dominates the algal population throughout hypersaline habitats [43].

Halophilic Bacteria

Halophilic bacteria are one of the most commonly isolated, reported, studied and characterised microbes amongst halophiles [44]. They exist in various forms of colonies, ranging from pigmented to non-pigmented, according to the salt concentration in the media. They are slow growing compared to non-halophile or normal bacteria. The extremely halophilic bacteria grow extremely slowly [45]. For *in vitro* culture on agar plates, most require natural brines along with a variety of other nutrients such as fish or milk extracts for their growth and a few of them also require complex nutrients like yeast extract for their survival. During the last few decades there was progress in providing a systematic base for classifying halophilic bacteria, including the use of various phenotypic characteristic tests and analytical apparatus. However, there are now taxonomically emerging groups of halophilic bacteria and their classification has not yet been much developed [46]. Salt characterisation for the optimum growth of halophilic bacteria is required prior to classification, but this step is costly, time consuming and is limited to only those cultivable and clonable isolates. A test methodology for halophilic bacteria has been recommended in which the media must be added with salt and the incubation time for subsequent growth is then assessed [47].

The taxonomy of halophilic bacteria was historically based on just a few phenotypic or morphological characters and less attention was paid to the phylogenetics or biochemistry of the organisms [47-49]. Phylogenetic analyses, largely based on the 16S rRNA gene sequence, have revealed that halophilic eubacteria and halophilic archaeobacteria are from different phylogenetic branches. Halophilic bacteria are generally represented by archaeobacteria, which are also comprised of the slightly and moderately halophilic bacteria, but most of these bacteria are eubacteria [14].

In hypersaline environments extremely halophilic bacteria and moderately halophilic bacteria are the important groups that have received most of the attention in recent research [44]. Slightly halophilic bacteria have been reported in studies focused on habitats such as the Dead Sea, GSL, Lake Magadi, Wadi El Natrun and some other extreme hypersaline environments that yield extremophilic bacteria. Slightly halophilic bacteria form a smaller proportion of the population in these environments and typically cannot be found in these harsh habitats [50]. The other drawback of characterising slightly halophilic bacteria is their characteristics that resemble the non-halophilic or normal bacteria, and these are typically of a lower interest for research. Due to the lack of sufficient information on the slightly halophilic bacteria, only a description of moderately and extremely halophilic bacteria is provided in this review.

Extremely halophilic bacteria

Extremely halophilic bacteria belong to the class *Halobacteria*, family *Halobacteriaceae* and order *Halobacteriales* [11]. Fourteen genera of Halobacteriaceae family are recognised, namely

Haloarcula, *Halobacterium*, *Halobaculum*, *Halococcus*, *Haloferax*, *Halogeometricum*, *Halorubrum*, *Haloterrigena*, *Natrialba*, *Natrinema*, *Natronobacterium*, *Natronococcus, Natronomonas* and *Natronorubrum*. They are coccii or rod-shaped and have a number of disk- to triangle-shaped involutions. They need salt concentration of 1.5 M (~8.8%) NaCl for their growth and lack muramic acid but possess peptidoglycan in the cell envelop. The colonies are highlighted by shades of red colour due to the presence of optically active C_{50}-carotenoids. Their intracellular enzymes require high levels (3–5 M) of potassium chloride whilst their cytoplasmic membranes are composed of phytanyl ether lipids. They show a degree of resistance against many antibiotics and occur in hypersaline environments such as salterns, soda lakes and salt lakes [45].

Moderately halophilic bacteria

Halophilic bacteria requiring a salt concentration of 0.5 M NaCl for their growth are included in the moderately halophilic bacteria group. Taxonomically, the moderately halophilic bacteria can be divided into the two groups: moderately halophilic eubacteria and moderately halophilic archaeobacteria [18].

Most of the bacterial halophiles are moderately halophilic eubacteria rather than extreme halophiles [6], and are phototrophic or heterotrophic, the latter including Gram-positive and Gram-negative bacteria. Gram-positive moderately halophilic species include *Deleya halophila*, *Desulfovibrio halophilus*, *Desulfohalobium retbaense*, *Flavobacterium halmephilum*, *Haloanaerobacter chitinovorans*, *Haloanaerobium praevalens*, *Halobacteroides halobius*, *Halomonas elongate*, *Halomonas eurihalina*, *Halomonas halodenitrificans*, *Halomonas halodurans*, *Halomonas subglaciescola*, *Paracoccus halodenitrificans*, *Pseudomonas beijerinckii*, *Pseudomonas halophila*, *Spirochaeta halophila*, *Sporohalobacter lortetii*, *Sporohalobacter marismortui* and *Vibrio costicola*. The Gram-negative moderately halophilic species include *Halobius spp.*, *Marinococcus albus*, *Marinococcus halobius* and *Sporosarcina halophila*. Phototrophic moderately halophilic bacteria are *Ectothiorhodospira vacuolata*, *Rhodospirillum salexigens* and *Rhodospirillum salinarum* [18].

Except for the methanogens, all halophilic archaea are considered as extremely halophilic bacteria [6]. The composition of the membrane-bounded cytoplasm of moderately halophilic archaeobacteria is similar to that of extremely halophilic bacteria in having phytanyl ether lipids. They have a unique nutritional intake capacity and use methylotrophic substrates rather than acetate, carbon dioxide and hydrogen. The mode of respiration is strictly anaerobic [51]. The intracellular NaCl concentration is higher than most other bacteria (about 0.6 M or 3.5% NaCl), but this concentration is much lower than that in the extremely halophilic archaeobacteria. Species reported for moderately halophilic archaeobacteria include members of the *Methanohalophilus* genus, e.g. *M. zhilinae*, *M. portucalensis*, *M. mahii*, *M. halophilus* and *M. portucalensis* [52].

Halophilic Fungi

Since the last decade, a few fungi have been included in halophilic microorganisms. Fungi isolated from substrates with a low water activity (w_a) are considered as a xerophilic phenotype and are designated by the w_a potential in the medium rather than by their biochemical nature [53, 54]. Fungi were therefore considered as a xerophile if they were able to grow at a w_a of 0.85, as a result of the introduction of 17% NaCl or 50% glucose into the medium. Fungal isolates that can be grown *in vitro* at 3 M NaCl, with a w_a of 0.85, have been regularly isolated from the hypersaline environments around the globe and are now considered as halotolerant fungi. Those capable of growth at salinity of more than 1.7 M NaCl are designated as halophilic fungi [56], which have also been reported from agar baits, biofilms or biomats on the surface water of crystallisation ponds, in brine solutions, immersed woods, microbial mats and over or under some specified depth of soil present in hypersaline environments [3].

Fungi were first isolated from solar salterns in 2000 [7], followed by reports of fungi in many hypersaline environments around the world, although not restricted to any specific geographical location. Interestingly, a high fungal diversity has been observed in terms of their phylogenetics. Unlike halophilic bacteria, halophilic fungi cannot be clustered in separate phylogenetic groups [3]. Nutrients such as nitrogen and phosphorus, w_a, location and time of sampling and dissolved oxygen levels were found to be important factors in the growth of halophilic fungi when the distribution of fungal community structures as well as their abundance in environmental gradients were checked statistically [56].

The halophilic fungi that inhabit natural hypersaline environments show a halotolerant behaviour that is quite different from other prokaryotic halophiles. Most halophilic fungi do not need salt for their survival and they can grow in a salt concentration of any range. Halophilic fungi can be found in freshwater and sea water, including water with an almost saturated concentration of salt [57].

Most of the reported halophilic fungi from solar salterns have either been identified as new species or species from previous natural niches which have been unrecognised, or as those only known before as foodborne species or food contaminants. The total number of fungal orders is 106 [58], of which only 10 have been reported to have tolerance to a low w_a. Of these reported orders, the ability to grow at a low w_a is mostly exhibited by a single genus a few species of an order. However, in the orders *Capnodiales*, *Eurotiales*, *Dothideales* of *Ascomycota* and *Wallemia* of *Basidiomycota*, the halophilic character is expressed in many groups of the same order, and some of them are not even closely related in phylogenetic analyses [14].

When the taxonomic distribution of halotolerant or xerotolerant fungi was compared with that of pathogenic fungi, they were surprisingly found to belong to the same orders in the fungal kingdom. Thus, xerotolerance, pathogenicity and survival in a harsh or difficult environmental condition seem to have a common link. However, there are also some xerotolerant strains or species that do not appear to be pathogenic, and so it is possible that pathogenecity and xerotolerance are mutually built characters of some species [59]. Recently, reported halophilic fungi have mostly been observed in the *Aspergillus* genus [3, 56, 60-62].

Adaptation of Halophilic Microorganisms in Hypersaline Environments

Two broad mechanisms, 'salt in' and 'low salt in', are known for the adaptation of halophilic microorganisms to their hypersaline habitats [46]. In 'salt in' strategy, the aerobic halophilic archaea accumulate a high salt concentration within their cells, with K^+ being the dominant ion. This accumulation of K^+ and also generally a large Na^+ presence are maintained by different ion pumps and protein transportation, which is only possible at the expense of energy [46, 63]. The second approach is the 'low salt in' strategy. In this mechanism of adaptation the microorganisms maintain a low salt concentration in the cytoplasmic medium and they counteract the salinity to maintain intracellular activities at a normal basis with the use of compatible osmotic solute(s). The list of known compatible solutes is ever growing. They are capable of making water structures, are highly soluble, polar and mostly form zwitterions [46].

Polyextremophilic Behaviour of Halophilic Microorganisms

Some of the halophilic microorganisms also adapt to other extremes such as temperature and pH, where they have thermophile/psycrophile or alkalophile/acidophile characteristics respectively [64]. Halothermophilic bacterium such as *Halothermothrix orenii* [65, 66] and *Acetohalobium arabaticum* [67] shows adaptation to a temperature of 50–68^{o}C. Psycrophilic-halophilic bacteria such as *Halorubrum lacusprofundi* have been reported from Antarctica [68, 69]. Halophilic archaea mostly impart the red colour observed in hypersaline soda lakes at a pH of 10–11 [52], while many haloarchaeal strains have been reported to grow at an acidic pH of 4–6 [70].

In the Natrun Valley of Egypt thermophilic/alkalophilic/halophilic bacteria such as *Natranaerobius thermophiles*, *Natranaerobius trueperi* and *Natronovirga wadinatrunensis* have been isolated that are capable of growing at 51–53^{o}C, pH 9.5–10 and 3.7–3.9 M Na^{+} [71, 72].

Biotechnological Applications of Halophilic Microorganisms

Some recently reported studies of biotechnological applications of halophilic microorganisms are summarised in Table 1. Halophilic microorganisms contribute to a better understanding of the interactions in simple ecosystems occupied by few inhabitants, increase our knowledge of stress responses and can help in identifying genes that enhance the functions of microbes used in industry [4, 5]. However, the biotechnological applications have been mostly limited to the use of halophilic bacteria, while the wide potential of the halophilic fungi has been neglected [4]. The latter not only can replace the halophilic bacteria in industrial use, but can also extend the number of applications of halophilic microorganisms.

Table 1. Some recent examples of biotechnological applications of halophilic microorganisms

Application	Reference
Antibiotics	[85, 86]
Antioxidants	[87]
Bioplastics	[47]
Bioremediation	[79, 83]
Environmental indicator	[5]
Halophilic amylases	[88]
Halophilic cellulases/xylanases	[89, 90]
Halophilic proteases	[80, 91]

Halophilic microorganisms, by themselves, are very useful microorganisms for at least two reasons. The first is the participation of halophilic microorganisms in the biogeochemical cycles of carbon, nitrogen, sulfur and phosphorus, the production of nutrients and the balance of ions [13]. The second reason is that because of their simple mode of nutrition, the majority of them can survive on just carbon as a single source of energy [73].

Halophilic microorganisms posses natural processes for the production of compatible solutes which, as osmolytes, have a number of potential applications. Some of the compatible solutes, especially the betaines, ectiones and glycine, can be utilised as stress protection against thermal denaturation, freezing, dessication, high salinity and a low w_a [74]. They can also be used as stabilisers of nucleic acids, membranes, complete cells or enzymes [75]. The use of these compatible solutes in the enzyme industry is very promising [76]. Some of the compatible solutes such as glycerol, ectoines, trehalose, proline, and glycerol and hydroxyacetone have shown a high degree of protection for the enzyme dehydrogenase during excessive cooling or heating. Ectoin has been reported as an efficient stabilising factor for freezing or cooling of phosphofructokinase [77]. Similarly, the uses of halophilic microorganisms in the production of biorhodopsin, biosurfactants for improved biodegradation processes and optical computing, exopolysaccharides for enhanced recovery of oil, food additives and compatible solutes as stress protectants have been reported [78, 79].

There has been an increasing interest in research on halotolerant enzymes owing to the fact that there is a large number of potential applications of these catalysts which can work in a low w_a condition [80]. Many halophilic enzymes have been found to be alkalophilic and thermophilic as well [81]. Halophilic microorganisms produce hydroxyalkanoates, which can be applied to the thermal processing of plastics [47]. For example, shear-, pH- and heat-resistant exopolysaccharides have been reported from *Haloferax mediterranei* [44].

Halophilic microorganisms can be used in bioremediation processes [5, 82, 83]. They have been found to facilitate the uptake of nutrients as well as induce salt tolerance amongst halophytes [74, 75, 82]. These microorganisms can also be used as an indicator for soil and water salinity [84]. The extracellular enzymes obtained from them can convert heavy biopolymers into more simple compounds.

The increasing problems of water scarcity and salinity also make halophilic microorganisms an important choice for obtaining tolerant genes which might be incorporated into food crops to enable them to grow in harsh conditions [4, 8, 10]. A recent research by our group has highlighted the antioxidant, antibacterial and enzymatic potential of obligate halophilic fungi isolated from man-made solar salterns in Thailand [4, 5].

CONCLUSIONS

We have tried to report the most simplified available information on halophilic microbes and their adaptation to their habitats. The polyextremophilic behaviour of halophilic microorganisms makes them particularly interesting microbes while new studies on halophilic fungi and their metabolites reveal them to be a potentially good choice in biotechnological applications and may possibly replace halophilic bacteria in industry. There is very limited information on halophilic algae and this needs further research.

In this era of climate change where extremes of weather can be experienced, halophilic microorganisms emerge as important choice for research to understand how they adapt themselves in extremes of physical conditions, which in turn can help humans nurture their food crops in the extremities of temperatures, pH and drought.

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