

Biodiversity of Hypersaline Environments

Subjects: Microbiology

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Halophiles are the salt-loving organisms. They are found in all three domains of life, namely Archaea, Bacteria, and Eukarya, and occur in saline and hypersaline environments worldwide. They are already a valuable source of various biomolecules for biotechnological, pharmaceutical, cosmetological and industrial applications.

Keywords: halophiles ; biomolecules ; metagenomics ; biodiversity ; hypersaline environments

1. Introduction

Halophiles are a highly miscellaneous class of extremophilic organisms characterised by their requirements for high salinity and comprise entities from all three domains of life, namely Bacteria, Archaea, and Eukarya ^{[1][2]}. Owing to their phylogenetic origin and the nourishment acquisition manner, halophilic microorganisms can be grouped as follows: (1) heterotrophic, phototrophic or methanogenic archaea; (2) heterotrophic, lithotrophic or photosynthetic bacteria, and (3) heterotrophic or photosynthetic eukaryotes ^{[2][3][4]}.

Due to the salt concentration requirements (specifically and commonly, sodium cations and chloride anions), halophiles can be classified as slight, with optimal growth at 0.2–0.85M (1–5%) NaCl, moderate thriving in 0.85–3.4M (5–20%) NaCl, and extreme growing optimally at 3.4–5.1M (20–30%) ^[5]. On the contrary, non-halophiles do not grow in the environment containing above 0.2M (1%) NaCl, and halotolerant organisms are viable in the presence or absence of highly saline conditions, but it is not necessary for their optimal growth ^[5]. Moreover, halophilic and halotolerant organisms are able to adapt to a broad range of salt concentrations, occurring seasonally, annually, or irregularly in their natural environments ^{[4][6]}.

Halophilic microorganisms are forced to efficiently prevent osmosis due to the high external salinity, and thus they have evolved two types of strategies to struggle with cellular water loss—“salt-out” (“low-salt-in”) and “salt-in” ^{[4][7]}. The first strategy is based on biosynthesis (*de novo* or from the storage substances) or absorption from the environment compatible solutes (osmolytes or osmoprotectants) and is utilized mainly by moderate halophiles, halotolerant bacteria, and eukaryotes. Polyols, sugars, amino acids, betaines, ectoines, N-acetylated diamino acids, and N-derivatized carboxamides of glutamine are commonly used. The second strategy relies on the accumulation of salt, predominantly potassium chloride, to provide intracellular osmotic pressure comparable to the external one and is typical for extremely halophilic Archaea and a few representatives of Bacteria (genus *Salinibacter* and members of the order *Halanaerobiales*) ^[2]. This mechanism requires specific adaptation of enzymes and other proteins, e.g., by elevating a level of negatively charged amino acids, leading to the formation of an acidic proteome as observed in *Halobacterium* sp. NRC-1 ^{[7][8][9]}. However, the evidence provided by Elevi Bardavid and Oren (2012) suggests that this may not be a strict rule, and other mechanisms must be involved in osmoregulation in halophiles ^[10]. Some halophiles (especially from the archaeal class of *Halobacteria*) have applied a mix of these strategies to cope mainly with periodic fluctuation of salinity ^{[11][12]}.

2. Global Distribution of Hypersaline Environments

Although the oceans and seas (average salinity–0.6 M, 3.5% or 35 parts per thousand) come to mind first, the term “hypersaline environments” refers to conditions where the salt concentration exceeds that present in marine basins (even ten times up to or above salt saturation) ^{[13][14]}. Hypersaline environments are generally classified as thalassic (thalassohaline) when originating from seawater with its characteristic ionic composition (dominated by Cl[−]—49% and Na⁺—42% of the total molarity) and as athalassic (athalassohaline, also inland or epicontinental) not directly associated with a marine source and dominated by divalent ions mainly Mg²⁺ and Ca²⁺ ^[5]. Some authors also distinguish the third type—artificial reservoirs employed for salt production (saltern crystalliser ponds) ^[15].

Nevertheless, hypersaline ecosystems and their habitats are widely explored mainly due to their utilisation in mineral processing—salt mines, solar salterns and salt flat ^{[16][17][18]}, aquaculture (e.g., brine-shrimps predominantly in the Great

Salt Lake, commercial lakes in China, Russia, and Kazakhstan [19][20], biotechnical applications (biomolecules like enzymes, pigments, antimicrobial agents, nanoparticles) [21][22][23][24]; in the role of microbial cell factors [25]; environmental and protection studies as niches for eukaryotes, prokaryotes, and archaea [15][17][26][27], biodegradation of contaminants [28][29][30][31]; astrobiological signification and early Earth connotations [32][33]. On the other hand, issues related to the anthropogenic impact on hypersaline environments have become more and more significant in recent years. To name only some: climate alteration, overexploitation of mining and mineral extraction, overflow of agriculture, water diversion and salinity enlargement, urban overdevelopment, industrial sewage and contamination with ultimate examples of the Dead Sea, the Caspian Sea, the Aral Sea, and the Great Salt Lake [15]. And as it turns out, these activities have a tremendous influence on the (bio)diversity of the hypersaline ecosystems.

3. Biodiversity of Hypersaline Environments

The Dutch microbiologist and botanist investigating various saline and hypersaline lakes worldwide Lourens G. M. Baas Becking (1895-1963) claimed that “*everything is everywhere: but, the environment selects*” [34]. This statement is highly relevant to the hypersaline ecosystems broadly distributed around the world, from the Antarctic to the Himalayas, from Australia to the USA, from Africa to South America, and thus are much dissimilar in terms of salt concentration, chemical composition, and presence of additional stress conditions designated by geological attributes [5][35][36][37]. Therefore, they are not only characterised by high-salt content but other environmental physicochemical extrema like high pressure and UV radiation, low oxygen concentration, hydrophobic conditions, extreme temperatures and pH, high concentrations of toxic compounds and heavy metals [27][36][38][39][40][41][42].

The most frequently identified bacterial phyla in saline and hypersaline environments are Actinobacteria, Bacteroidetes, Cyanobacteria, Proteobacteria (Alpha, Beta, Gamma, and Delta), and Firmicutes [36][41][43][44][45][46][47][48]. Halophilic Archaea are typically represented by Halobacteria and methylophilic methanogens class members, both belonging to the phylum Euryarchaeota. The former includes about 70 genera and 260 species, classified in three orders and six families: the *Halobacteriales* (families *Halobacteriaceae*, *Haloarculaceae*, *Halococcaceae*), the *Haloferacales* (families *Haloferacaceae*, *Halorubraceae*), and the *Natrialbales* (family *Natrialbaceae*), and the latter comprises of 4 classes: *Methanomicrobia*, *Methanobacteria*, *Methanopyri* and *Methanococci* [49][50]. Furthermore, it was demonstrated that Archaea tend to dominate Bacteria as salinity increases, which is illustrated by an excellent example of the two arms of the Great Salt Lake, significantly different in the salt content, and thus in a taxonomy of their inhabitants [36][37][51][52]. Moreover, the composition and structure of halophilic communities in saline and hypersaline ecosystems are considerably influenced by the salinity fluctuation in time or geographical location and may differ between the places of sampling within the same setting [53][54][55][56][57].

Saline soils are other fascinating and valuable from the ecological, economical, and biotechnological points of view examined environments with abundance and high diversity of their inhabitants, taxonomically comparable to aqueous ones (phylum level) [58][59]. In addition, it has been established that salinity, along with pH and electrical conductivity (EC), are the pivotal factors determining the variety and arrangement of halophiles and haloalkaliphiles in saline soils [60][61][62]. Intriguingly, these microorganisms are gaining special attention due to progressing global soil salinisation, and thus their potential applicability as plant symbionts enabling and increasing crop productivity in saline soils [63][64]. It is noteworthy that a successful attempt was currently done to employ halophilic microorganisms as bioindicators of the soil salt contamination caused by extensive de-icing of roads during harsh winters in Baltimore, Maryland, USA. It became possible since halophiles become persistent members of microbial communities as a result of salting roads for their de-icing during winter months [65].

In addition to these environmental species, there is a constantly extending group of human or human-related halophiles, both bacterial and archaeal [66][67][68][69]. Brining, i.e., treating, food with dry salt or a salt solution, is one of the oldest methods to preserve and season the eatables in food processing. There are numerous and continual scientific reports on isolating new halophilic microorganisms, the diversity and properties of halophilic Bacteria and Archaea, as well as genomic analyses from commercial salt [70][71][72][73], cheeses [74][75][76][77], table olives [78], kimchi (Asian fermented vegetables) [79][80][81], and shrimp paste [82][83]. Recent years have also brought interest in the halophilic and halotolerant prokaryotes contributing to the human gut microbiota [73][84][85][86]. This attention results in part from observing a hazardous tendency to consume increasing amounts of salt delivered with food and its tremendous consequences on human health, including obesity, hypertension, cardiovascular disorders, and stomach cancers [69].

Finally, halophilic prokaryotes are the established producers of multiple biomolecules and chemical substances, predominantly osmolytes, hydrolytic enzymes, and pigments (e.g., carotenoids) [22][87][88][89][90]. The increasing interest in compounds and proteins of halophilic origin results mainly from the fact that they remain active under harsh conditions like

high salinity, extreme temperatures, and ultimate pH [91]. Moreover, halophilic enzymes retain solubility and solvation in low water activity [11], and as has been shown recently, they demonstrate anti-desiccation and antifreeze properties, so desirable in food processing and preservation [88]. Halophiles also produce biodegradable polysaccharides and polymers, potentially replacing environmentally hazardous plastics; glycoproteins are considered promising candidates in nanoparticles synthesis, and gas vesicles are examined in terms of an effective drug delivery system as described thoroughly in a review released by Singh and Singh, 2017 [90]. Despite that, bacterial and particularly archaeal halophiles for decades have been underestimated and unexplored in terms of the ability to produce various bioactive compounds, especially of antimicrobial and anticancer potential. However, due to the rapid development of molecular techniques, they turned out to be a promising and rich source of diverse biomolecules of great importance in the ongoing post-antibiotic era that is additionally characterised by the galloping increase of cancer cases [22][91][92][93][94][95]. Due to methodological difficulties, time-consuming and expensive procedures that require frequent optimization and the increasing availability of sequencing, research on halophilic biomolecules are moving more and more towards genomic and metagenomic-based bioinformatics analyses [96][97][98][99][100][101].

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