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Marine Extremophiles

Adaptations and Biotechnological Applications

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74.1 Extremophiles

The ideal life for living organisms is in common terms reported to be as survival under a predefined range of parameters such as temperature about 30 to 40°C, pH strongly recommended as neutral, pressure of around 1 atm, sufficient availability of nutrients, water content and tolerable radiation energy (Kazak, 2010). Other intolerable or lethal conditions as compared to the aforementioned ideal atmosphere is defined as an extreme environment. Natural systems like soda lakes, salt pans, oceans, deserts, deep thermal vents and hot springs possess such extreme environments that they are said to be non-survivable for all the living organisms (Satyanarayana, 2005). Extreme environments are also considered as highly fluctuating in physical conditions like temperature, pH, pressure, nutrient availability, radiation, salinity, etc. However, several microorganisms both eukaryotes and prokaryotes, are known to survive these conditions and such organisms are called as extremophiles. The idiom *extremophiles* was originally coined by MacElroy in 1974 (Horikoshi, 1998a). This diverse group of organisms, identified as extremophiles, not only tolerate extreme conditions, but require these environments for their endurance and development. The knowledge of the presence of extremophiles in extreme environments encouraged studies focused on their evolution and environmental science. Higher organisms are unable to endure these extreme environments, thus investigation on extremophiles has included maximum attention on Bacteria and Archaea (Kazak, 2010). Extremophiles are named and classified according to environmental changes under which they survive (Table 74.1).

For the adaptation in extreme environments, many organisms have developed unique characteristics. These adaptive strategies are considerably important in various significant biotechnological applications. Extremophiles are elite suppliers of various biopolymers, extremozymes etc.; one of the examples includes soil degrading extremozymes used in pollution removal via an eco-friendly biological approach. Other novel products of extremophiles are used in treatment of coal and waste gas, bioleaching, as molecular sieves, in drug delivery, cosmetic

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Table 74.1 Major classification and subtypes of extremophiles based on their environmental habitat.

Environmental conditions	Types of extremophile	Limitations for growth
	Hyperthermophile	High temperature > 80°C
	Thermophile	Range of 60–80°C
Temperature	Mesophile	Normal 15–40°C
	Psychrophile	Very low temperature <15°C
pH	Acidophile	Require pH ≤ 3.0
	Alkalophile	Require pH ≥ 9.0
Salinity	Halophile	Salt-loving organisms
Pressure	Barophile	Grown in high pressure
Radiation	Radiophile	Requires radiation for growth
Desiccation	Xerophile	Low water availability
CO_2 requirement	Capnophile	CO_2 available conditions
Nutrient availability	Oligotrophile	Low concentrations of nutrients

packaging, etc. Salt loving organisms are used in bioelectronic optical switches, photocurrent generators and in production of biodegradable plastics. Ectoine is significantly obtained from halophiles, and this product is used as an osmotolaprotectant, stabilizer and mainly in skin treatment. Some important *extremozymes* such as alkaline phosphatases and DNA polymerases are used in diagnosis, while lipases, pullulanases, proteases and amylases are used in the dairy industry; protease is mainly used in contact lens solutions, and oxidase is mainly used as a biosensor. These are commonly obtained from extremophile sources.

74.2 Types of Extremophile and their Adaptations

74.2.1 Temperature

Microbes that survive and grow below 15°C and above 80°C are classified as thermophilic extremophiles. Based on the temperature gradient in a habitat organisms are classified into four main classes: A. Hyperthermophiles; B. Thermophiles; C. Mesophiles; and D. Psychrophiles.

74.2.1.1 Hyperthermophiles

Hyperthermophilic organisms are also called super heat loving organisms because they can withstand temperatures above 80°C. Discovery of the first hyperthermophilic life viz., *Sulfolobus acidocaldarius* was from Yellowstone National Park by Thomas Brock in 1972. Recent reports have mentioned that around 90 species are identified as thermophilic organisms (Statter, 2013). Hyperthermophiles mainly belong to the Archaea domain and some of them are Bacteria. One study reported a thermophile (optimum growth at 110°C) *Methanopyrus kandleri*, from the Gulf of California. The same species *M. kandleri* was later also isolated from the Kairei vent field of the Central Indian Ridge, and grew at 122°C. Previously, *Geogemma barossii* strain 121 was recorded at a growing temperature of 121°C.

Organisms have developed various strategies to grow and survive with temperature variation. Step-wise adaptation to temperature was observed in organisms; a strategy called thermal adaptation. The tRNA genes in the hyperthermophiles are rich in GC content compared to thermophiles, mesophiles and psychrophiles. High GC content might be contributing to stabilization of intramolecules and RNA secondary structure in extreme temperature (Avirup, 2010). At the protein level, frequency of amino acids is less in the case of hyperthermophiles, and may be involved in imposing thermal stability in the form of heat shock proteins. Jaenicke and Bohm (2001) reported this type of protein stability in a strain of *Thermotoga maritime*. Modifications in nucleoside sequence in the post-transcriptional stage of tRNA preparations of hyperthermophiles is one of the important variations for adaptation, as this modification gives higher stability in restriction observed in ribose rings, and favors the A-type helix present in phosphodiester bond hydrolysis (Cummins, 1995). Horizontal gene transfer (HGT) is one of the well-known adaptions for adaptation in elevated temperature, whereby the DNA is repaired by transferring DNA. In many species of bacteria and Archaea, different transfer mechanisms have been reported in hyperthermophilic conditions.

74.2.1.2 Thermophiles and Mesophiles

Optimum temperature for survival and growth of mesophilic organisms is around 15–40°C and for thermophiles it is 60–80°C. Thermophiles are more common than hyperthermophiles, and are represented by a higher number of species including enterobacteria like *Bacillus*, *Clostridium* etc., photosynthetic bacteria like cyanobacteria, green purple bacteria, Archaea bacteria like *Thermoccocus, Pyrococcus*, methanogens, *Sulfolobus* and thionic bacteria like *Thiobacillus* (Vieille, 2001). Two of the most common habitats from where thermophiles survive in the optimum range of 80°C to 122°C include the hydrothermal vents and hot springs across the globe, where species belonging to the genera *Pyrococcus*, *Thermocrinis*, *Hyperthermus*, etc have been observed (Clarke, 2014). According to the hypothesis of Hamana et al. (2003) thermophiles are descended from mesophiles for adaptation to elevated temperature.

Structural changes in membrane lipids such as in acylation, branching, saturation and the formation of unique hydrocarbon chains are observed in thermophilic bacteria compared to mesophiles (Morozokinaa, 2010).

- High concentration of binding proteins with positively charged DNA and high GC content provides resistance towards DNA denaturation at high temperatures.
- Detection of *rgy* gene (reverse gyrase) in thermophilic bacterium *Thermococcus kodakaraensis* KOD1 provided protection up to temperature of as high as 90°C.
- Increase in the level of intracellular electrolytes such as cellular polyamines is only found in thermophiles while in mesophiles it is absent (Kneifel, 1986).
- High molecular weight heat shock proteins (HSP) are also uniquely observed in thermophiles and hyperthermophiles. These proteins prevent protein aggregation, refold the denaturated proteins and also synthesize structurally diverse new proteins under high temperature (Van Montfort, 2001).
- HSP increased the thermostability of cell proteins but the sequence and structures are somewhat similar as reported by Taylor in 2010. The protein structure of thermophilic *Pyrococcus woesi* and mesophilic *Saccharomyces cerevisiae* is similar; they share the same catalytic action and are active at high temperatures whereas at low temperature activity is lowered or totally hindered.

74.2.1.3 Biotechnological Applications of Hyperthermophiles, Thermophiles and Mesophiles

Thermophiles and their products are mainly used in industry because of their catalytic activity and thermodynamic reactions at high temperature. Another benefit being that at elevated temperature, the chances of contamination are extremely low and thus, they can be applicable in the food and drug industries. The first application was the production of Taq DNA from polymerase from the thermophilic bacterium *Thermus aquaticus* used in the biological laboratory for PCR amplification

Table 74.2 List of thermophilic organisms and their applications.

Name of the organisms	Thermostable product	Applicable fields	References
Thermus aquaticus	Taq DNA polymerase	Biological research	Unsworth, 2007
Pyrococcus furiosus	Amylase enzyme	Food, cosmetic and pharmaceutical fields	Park, 2013
Bacillus stearothermophilus	Glucokinase	Used as bioindicator	D'Auria, 2002
Clostridium cellulovorans	Cellulosome-production	Biofuel production	Yutaka, 2010
Sulfolobus tokodaii, Bacillus thuringiensis	Chitinase	Biofungicide and bioinsecticide	Staufenberger, 2012
Coprothermobacter proteolyticus	Protease	Detergent, food, leather, pharmaceutical, and textile industries	Li, 2013
Caldimonas taiwanensis sp. nov., *Haloarcula hispânica, Bacillus* sp., *Ferdowsicous*, *Geobacillus thermoleovorans*	α-amylases	Food, fermentation and pharmaceutical industries	Paula Monteiro, 2010
Tepidiphilus margaritifer strain N2-214, *Bacillus fumarioli* strain LMG 18418	Lignocellulolytic enzyme	Lignocellulose degradation aspect	Sarunyou, 2010

(Unsworth, 2007). Amylase enzyme extracted from *Pyrococcus furiosus* is being used as a carrier in the food, cosmetic and pharmaceutical fields (Park, 2013). (See Table 74.2.)

74.2.2 Psychrophiles

From all the extreme conditions on Earth, psychrophiles are profuse in terms of diversity, biomass and distribution. On the Earth, >80% of biosphere is cold (frozen area) with a permanent temperature below 5°C. Below 1000 m depth, the ocean temperature is 2–4°C; alpine and glacier-like polar regions and permafrost (15% and 20% of the earth) are among the other cold regions. These very low temperature regions are well colonized by organisms; as a result psychrophiles are plentiful on earth. Life at low temperature requires unique survival strategies in the cellular system of organisms, which developed modified architecture in the cell by producing structurally novel and diverse proteins, as well as cold-active enzymes. These cryo-enzymes are quite unique from others. Several species of *Shewanella* with the genome size of 4.5 to 5.5 Mb have been isolated from the Baltic Sea and Antartic regions. *Psychrobacter* is the other dominant genus isolated and screened from the permafrost areas; others include *Halorubru, Methanococcoides, Photobacterium, Sphingopyxis, Desulfotalea, Polaribacter* and *Octadecabacter* and all have different genome sizes as small as 2.6 to 5.5 Mb (Casanueva, 2010). Psychrophilic bacteria modified their membrane by an increased ratio of saturated to polyunsaturated fatty acid, decrease in size of a charged group of lipids, and by alterations in the lipid class composition (Guan, 2013). According to comparative genomic studies, the genes responsible for cell membrane biogenesis are over-expressed in psychrophilic bacteria (Lauro, 2008). The genes which are responsible for the outer membrane proteins, flagella, and uptake receptors, are suppressed at low temperature (Durack, 2013). Membrane fluidity is the key adaptor for the cell in extreme conditions; here cold loving organisms maintain fluid in the homeoviscose stage (Rodrigues, 2008). The increase in concentration of compatible solutes like betaine, sucrose, lycine and mannitol, prevents cell crystallization and damage from low temperature. Some psychrophilic bacteria produce anti-freezing proteins (Kawahara, 2002).

74.2.2.1 Biotechnological Applications of Psychrophiles

Cold active products from psychrophiles are mainly used in food technology, molecular biotechnology research, pharmaceutical research and in medical fields, wherein these cold stable products are used for synthesis of novel antibiotics for cancer therapy and nutraceuticals. Nowadays, bioremediation and degradation aspects are also focused on in cold-adapted bacteria research. (See Table 74.3.)

74.2.3 pH

The majority of biological processes are done under neutral pH, but some unique organisms grow under high or low pH conditions. Depending on pH shift in environments; organisms are categorized into three types: acidophiles, neutrophiles, alkalophiles.

74.2.3.1 Acidophiles

Microorganisms withstand or grow under low pH (below 3 pH) conditions. In the leaching process, industrial effluents containing acids, acid mines etc, are a habitat for acidophiles. Among the these, mainly sulfur oxidizing bacteria, other different prokaryotic and eukaryotic species, some fungi such as *Trichosporon cerebriae, Acontium cylatium, Cephalosporium* sp., etc. have the potential to grow under pH 0.

- The main adaptive strategy of the cell is maintaining pH homeostasis. Acidophiles maintain cells near pH 4.6. By maintaining very low pH, the cell restricts the entry of protons by the cytoplasmic membrane, for survival in a low pH environment.
- There is an increase in the impermeability of the cell membrane for limiting influx of protons in the cell.
- In *Acidithiobacillus ferrooxidans*, protein pore size of the membrane channels is reduced, when pH shifts from 4.5 to 1.0.
- Another strategy to limit proton entry is by proton influx inhibition by the organisms creating chemosmotic gradient by using the Donnan potential. The mechanism is shown by many acidophiles, such *as Picrophilus torridus, Leptospirillum ferriphilum, Acidithiobacillus thiooxidans* and *Acidithiobacillus caldus*.
- In cases of sudden pH change, organisms pump out the protons by proton motive

Table 74.3 List of psychrophiles and their biotechnological applications.

Name of organisms	Cold active product	Biotechnological applications
Pseudoalteromonas haloplanktis	Monooxygenase	Degradation of aromatic hydrocarbons
Arthrobacter psychrolactophilus	Cold adapted proteins	Organic compound containing water treatment
Rhodotorula psychrophenolica	Monooxygenase	Phenol degradation
Pseudoalteromonas haloplanktis	Protease	Food industry
Pseudoalteromonas haloplanktis	α-Amylase	Dough fermentation, bakery products
Pseudoalteromonas haloplanktis	Glucanases	Animal feed for the improvement of digestibility

force. For acidophiles, high organic concentration in the cell is harmful, so cells uncouple the proton with the help of organic acids. The cell removes excess proton and organic acids.

- Acidophiles have unique chaperones for repairing DNA damage at low pH and have developed novel enzymes for cell stability.

(See Table 74.4.)

74.2.3.2 Alkalophiles

Microorganisms withstand or grow under high pH (more than pH 8) conditions. There are mainly two types of naturally occurring alkali environments: high Ca^{2+} includes ground water and low Ca^{2+} containing soda lakes and deserts have a high concentration of sodium carbonate. There are many locations such as Oman, California, Yugoslavia, Jordan, Turkey and Cyprus which naturally contain high Ca^{2+}. The industrial process of serpentinization releases high amounts of Fe^{2+}, creating alkaline conditions in the environment. Soda desert and lakes are a dominant alkaline environment in the world; in these environments Na_2CO_3 is in high concentrations. Soda lakes also contain Mg^{2+}, which gives buffering capacity to lake water. Other habitats in the surrounding areas near industry related to alkaline electroplating, food processing, KOH mediated removal of potato skins, cement manufacture, paper and board manufacture, leather tanning, rayon manufacture, herbicide manufacture, indigo fermentation, etc are involved in creating alkaline conditions due to the above anthropogenic sources (Zeynep, 2002). *Bacillus* and cyanobacteria are the most dominant in an alkali environment. Alkalophiles require alkaline conditions and sodium ions for growth, sporulation and germination. *Anaerobranca horikoshii* and *Anaerobranca gottschalkii* were isolated from Yellowstone National Park and Lake

Table 74.4 List of acidophiles from marine environments and their biotechnological applications.

Name of organisms	Enzymes	Applications
Acidithiobacillus ferrooxidans **pH 1.8** *Acidithiobacillus ferrooxidans* **ATCC23270** **pH 1.8** *Acidithiobacillus caldus* **pH 2.5** *Acidithiobacillus thiooxidans* **pH 2.5** *Leptospirillum* group II **pH 2** *Acidiphilium acidophilum* **pH 1.8** *Acidiphilium multivorum* **pH 3** *Acidiphilium cryptum* **pH 3** *Acidocella faecalis* **pH 2.3**	Amylases, glucoamylases, Proteases, cellulases and oxidases	Starch processing, feed component, desulfurization of coal, detergent, textiles, dye industry, metal leaching process, etc.

Bogoriae in Kenya. *Thermococcus alcaliphilus, Thermococcus acidoaminivorans, Thermococcus alcaliphilus* and *Thermococcus acidoaminivorans* were grown at pH 9 (Antranikian, 2005).

- Alkaliphiles maintain their internal neutral pH separately from the extracellular alkaline environment.
- In the cell wall, the content of acidic polymers increases, such as galacturonic acid, glutamic acid, aspartic acid, gluconic acid and phosphoric acid. In peptidoglycans hexosamines and amino acids are in excess amounts. These negatively charged acids in the cell wall increase the absorbance capacity for sodium ions for protection in high pH (Aono, 1983).
- Alkalophiles require pH 9–11 and Na^+ ions for growth; for absorption of Na^+ ions, cells use proton motive force as per chemiosmotic theory. They exchange H^+ with the Na^+. Organisms have a unique barrier to reduce pH value from 10.5 to 7.5 (Horikoshi, 1999).

(See Table 74.5.)

74.2.4 Halophiles

Halophiles are among the most diverse group of organisms requiring high salt concentration for growth known as the halophilic organisms, and those that can tolerate high salt concentration are called halotolerant. Halophiles contain all types of organism from three domains: Bacteria, Archaea and Eucharya and are classified into three classes (see Table 74.6).

Some halotolerant bacteria which cannot tolerate salt concentration above sea-water are: *Algoriphagus halophilus, Hongiella halophila, Terribacillus halophilus, Aestuariibacter halophilus, Arcobacter halophilus* and *Microbacterium*

Table 74.5 List of alkaliphiles and various biotechnological applications.

Name of organisms	Enzyme	Applications
Bacillus pumilus, *Bacillus licheniformis* strain, PWD-1, other *Bacillus* spp.	Protease	Detergent formulations, surfactants or other additives, silk degumming, food and feed industry (Gupta, 2002)
Bacillus halodurans A-59, *Natronococcus* sp. strain Ah-36, *Haloferax volcanii*	Amylase	Food industry, brewing, baking, processing of fruit juice, paper and textile processing (Sivaramakrishnan, 2006)
Bacillus sp. KSM-635	Cellulase	Key role in the finishing of fabrics and clothes (Sarethy, 2011)
Pseudomonas monteilii TKU009, *Burkholderia cepacia* LP08	Lipase	Detergent additives, oxidizing agents and surfactants (Horchani, 2009)
B. gibsonii strain S-2, *Bacillus* sp. GIR 277	Pectinase	Biocontrol agents of agricultural pests (Li, 2005)
Nocardiopsis albus ssp. OPC-131	Chitinase	Natural pigments preparation (Sivasankar, 2005)
Thermoleophilum album *Exiguobacterium oxidotolerans*	Catalase	Food-processing industries, genetic and protein engineering techniques (Yumoto, 2004)

Table 74.6 Classification of halophiles.

Slight halophiles	Require 2–5% of NaCl concentration for growth
Moderate halophiles	Require 5–20% of NaCl concentration for growth
Extreme halophiles	Require 20–30% or above of NaCl concentration for growth

halophilum (Das Sarma, 2002). The hypersaline environment is part of the ocean where salt concentrations are extremely high. The hypersaline environments are divided into two (Gillevet, 2002):

1) Thalassohaline environments – these contain high concentrations of NaCl and athalassic waters; also called non-marine water with high salt concentrations (Maturrano et al., 2006). Example – solar salterns (results from evaporation of sea-water).
2) Athalassohaline environments – contain ionic composition such as sodium, potassium and magnesium and sources of magnesium metal, soda, potash, borax (boron) (Gillevet, 2002). Example – neutral saline lakes with pH 6–8.5.

Habitats for halophiles include the Mono Lake (US), Great Salt Lake in western United States, Dead Sea in the Middle East, the Dead Sea, Lake Magadi in Kenya, Solar Lake, salt pans, Gavish Sabkha, Ras Muhammad Pool on the California coast, the alkaline soda lakes in Egypt, Lake Sivash Australia, Organic Lake, Deep Lake and Lake Suribati of Antarctica and other athalassohaline hypersaline systems (Gillevet, 2002). There are some soda lakes and deserts distributed worldwide; a few examples include those in Africa like the Wadi Natrun; Egypt: Lake Magadi; East Africa: Lake Natron, Lake Bogoria, Lake Chad; USA: Owens Lake, Searles Lake, Trona, Borax Lake, Union Pacific Lakes, Lake Texcoco; and the Caspian Sea region in Europe (Grant, 2006).

Halophiles are the most studied class of all the other extremophiles. They have novel strategies to withstand the saline conditions, which have been the subject of research on halophile studies. A few examples of common halophilic microorganisms found all over the world are: *Halomonas*, *Deleya*, *Flavobacterium*, *Natronobacterium gregoryi*, *Pseudomonas*, *Natrialba magadii*, *Volcaniella*, *Natronomonas pharaonis*, *Halovibrio*, *Paracoccus*, *Halorubrum vacuolatum*, *Chromobacterium*, *Halorhodospira* and *Halomonas* spp. (Bowers, 2011) (see Table 74.7).

In cell metabolism small organic molecules in the form of compatible solutes are responsible for providing osmotic balance. Compatible solutes are zwitter ionic or uncharged ions such as glycine and ectoine which are used as osmotic solutes in cell physiology (Oren, 2008; Roberts, 2005). In halophiles, when the external environment creates osmotic imbalance,

Table 74.7 List of halophilic Archaea isolated from marine sources.

Name of organisms	Source of isolation
Haladaptatus letorious	Solar saltern, Jiangsu, China
Haladaptatus paucihalophilus	Zodletone spring
Haloarcula amylolytica	Aibi salt lake, China
Haloarcula argentinensis	Saltern soil, Argentina
Haloarcula hispanica	Marine salterns, Spain
Haloarcula japonica	Saltern soil, Japan
Haloarcula marismortui	Dead Sea
Haloarcula quadrata	Brine pool, Egypt
Haloarcula vallismortis	Death valley
Halobacterium noricense	Salt mine, Australia
Halobacterium piscisalsi	Salt mine, Australia
Haloplanus natans	Dead sea
Halorubrum arcis	Salt pans, Tibet
Halorubrum coliforniense	Solar plant, California
Halorubrum luteum	Salt lake, China
Halorubrum orientale	Salt lake, China
Halorubrum chaoviator	Salt brine, Mexico

bacteria accumulate these compatible solutes for balancing cell viability. They also maintain structure, solubility and stability of significant protein in cell membranes in highly saline environments (Empadinhas and da Costa, 2008). (See Table 74.8.)

Cytoplasmic membrane in bacteria is permeable for the ions, water, organic or inorganic material, but it is specific for some solutes (Poolman and Glaasker, 1998). Water flow is always from low to high activity, but when the external environment is highly saline, the turger pressure is increased and the cell system, physiology, and structure of biomolecules tends to change or alter (Wood et al., 2001). Either the cell wall is damaged or ruptured, or death of the cell occurs; halophiles face both problems on account of high salt concentration and low water activity. At this time halophiles exceed the intracellular solute concentrations and build up more compatible solutes with K^+ ions, for increasing the strength of the cell and preventing cell death. This mechanism was first researched by Kempf and Bremer in 1998.

- In halophiles, K^+ ion concentrations increased with the increase in salinity in the external environment. By this altering cell system, the cell can maintain turger pressure and osmotic stress (Empadinhas and da Costa, 2008).
- Halophiles have two main strategies for surviving osmotic stress and for maintaining osmoregulation in high salt concentrations: the first one is a salt-in-cytoplasm mechanism; in this type of strategy they increase the accumulation of inorganic ions, most importantly the concentration of K^+ and Cl^-. Intracellular enzymatic machinery is modified when the cell's internal saline concentration is increased. The mechanism is used by some halophiles belonging to the family Halobacteriaceae, including genera such as *Haloquadratum, Halobacterium, Haloarcula, Natronobacterium, Halorhabdus* and *Natronococcus* (Pflüger and Müller, 2004; Oren, 2002). The second mechanism is called the salt-out-cytoplasm mechanism, and is very widely found in all organisms. The name itself suggests that it excludes the extra salt from the cell and accumulates compatible solute, maintaining osmoregulation. In this type of mechanism no major alteration is observed in cell machinery and enzyme activity (Galinski and Trüper, 1994).
- Compatible solutes are also called osmo-protectants. In some halophiles, osmo-protectant is synthesized by the cell as required, such as ectoine, glycine and betaine. In some cases osmo-protectants are taken up from the surrounding medium of the environment (Oren, 2008; Oren, 2002).

Table 74.8 Allotment of common compatible solutes in halophiles.

Compounds	Occurrence
N-Acetyl-β-lysine *N*-δ-Acetyl-ornithine	Unique to methanogenic Archaea, *Sporosarcina halophila*
Ectoine and hydroxyectoine	Halophilic/halotolerant *Bacillus* strains, *Ectothiorhodospira halochloris*, aerobic heterotrophic bacteria, most halophilic proteobacteria, *Micrococcus* spp., *Bacillus* spp., *Marinococcus* spp., *Halobacillus halophilus*
α-Glutamate	*Halobacillus halophilus*
Glycine betaine	Archaea (universal compatible solute)
Proline	halophilic/halotolerant *Bacillus* strains

74.2.4.1 Biotechnological Applications of Halophiles

Halophiles are the most diverse group having unique adapting strategies, and have various biotechnological applications. One of the important halophilic green algae *Dunaliella* produced a high amount of glycerol and β-carotene, which is applicable in the food, pharmaceutical and chemical industries (Ventosa and Nieto, 1995). β-carotene is highly in demand as an antioxidant and food coloring agent. *D. salina* and *D. bardawil* are rich sources of β-carotene and pigment and are produced in the form of small globules in between thylakoids and the cell membrane (Ye, 2008). Some other bacteria such as *Halomonas elongate* and *Pantoea agglomerans* are also known to produce β-carotene (Rodriguez-Saiz, 2007). Biosurfactant production from halophilic and halotolerant bacteria containing trehalose lipids, mainly obtained from marine *Rhodococci* spp., is applied in microbial enhanced oil recovery (MEOR) and *in situ* bioremediation (Yakimov et al., 1999).

Exopolysaccharides (EPSs) produced from halophilic bacteria are applied in dye removal, the food industry, and the pharma industry for capsulation coating, etc. Some species of halophilic bacteria such as *Halobacterium salinarum, Halobacterium distributum, Haloferax volcanii, Halomonas eurihalina* and *Aphanocapsa halophytica* produce EPSs (Margesin and Schinner, 2001). Liposome production from *Halobacterium cutirubrum* which produces novel ether lipids, are applied in cosmetics and as medicines for transportation of specific biomolecules in disease treatment (Litchfield, 2011). The first report of polyhydroxyalkanoates (PHA) (that are biodegradable and biocompatible in nature) was from a marine halophile. It is a chain of polyester accumulating in the cell membrane as lipid moieties, and is mainly used in biofuel, bioplastics and the pharma industry (Chen and Patel, 2012). Haloarchaea *Haloferax mediterranei* and *H. volcanii* produce PHA bioplastics (Fernandez-Castillo, 1986). *Haloferax mediterranei* and *Halomonas boliviensis* produce PHAs and osmotic solutes (Quillaguamán, 2010). Halophiles produce ectoines as compatible solutes for osmoregulation; nowadays these ectoines are used as protectants in many industries. Also, they are protectants to preserve DNA, protein and other mammalian cells (Pastor et al., 2010). Moderate halophiles *Halomonas elongata, Halomonas salina, Chromohalobacter salexigens, Marinococcus* M52, *Methylarcula marina* and *Methylarcula terricola* are reported to produce high amounts of ectoines (Yin, 2015). Production of hydrolases from halophiles are the most common applications. Many halophiles secrete extracellular enzymes, which include the group of hydrolases which is a cluster of cellulases, amylases, proteases, lipases and xylanases. These hydrolases have the capability to conduct hydrolysis reactions under high salt concentrations, so these enzymes are highly stable and reactive in extreme conditions. (See Table 74.9.)

Other than these enzymes DNAses, pullulanases, pectinases , lipases, chitinases and inulinases are commonly produced by halophiles and applicable in many industries (Makhdoumi Kakhki et al., 2011). From halophiles, reports describe production of various antibiotics with antitumor activity and biopesticides with agricultural applications (Singh, 2010). *Halomonas* spp. produced a unique antibiotic, aminophenoxazinone (Bitzer et al., 2006). Some types of halophilic Archaea produced membrane-bound pigments; halorhodopsin and bacteriorhodopsin (BR). These pigments are used as light for energy production. Some bacteria such as *Halobacterium salinarum* and *H. halobium* are widely applicable for pigment production. BR is mainly applicable as a bioelement in biocomputers. It is also applicable as a light energy converter in various industrial areas (Kikura et al., 1998).

74.2.5 Barophiles/Piezophiles

The high pressure-philic organisms are called barophiles. The optimal ranges of barophiles

Table 74.9 List of enzymes from halophiles and their applications.

Name of enzyme	Name of organisms	Applications	References
Amylases	*Micrococcus halobius*, *Halomonas meridiana*, *Halobacillus* spp., *Halothermothrix orenii*, *Streptomyces* sp., and *Chromohalobacter* sp.	Treatment of waste water high salts and starch residues	Chakraborty et al., 2009 and Margesin and Schinner, 2001
Proteases	*Bacillus* spp., *Pseudoaltermonas* sp., *Salinivobrio* sp., *Halobacillus* spp., *Filobacillus* sp., *Chromohalobacter* sp., *Nesterenkonia* sp., and *Virgibacillus* sp.	Laundry additives, pharmaceuticals, Waste management and food processing	Karbalaei-Heidari et al., 2009; Vidyasagar et al., 2009 and Moreno et al., 2009
Xylanases	*Glaciecola mesophila, Chromohalobacter* sp., *Nesterenkonia* sp., and *Bacillus pumilus* GESF-1, *Zunongwangia profunda*	Biobleaching of paper and pulp	Mamo et al., 2009; Setati, 2010, Menon et al., 2010 and Liu et al. 2014
Cellulases	*Salinivibrio* spp., and *Halomonas* spp.	Textile processing, bioethanol production, textile, laundry and food industries	Wang et al., 2009, Shivanand et al., 2013

for growth observed are 70–80 MPa and 100–200 MPa. If the pressure decreases to about 50 MPa, organisms critically survive (Abe and Horikoshi, 2001). The main habitat for barophiles is the bottom of the ocean, which contains extreme hydrostatic pressure and very low temperature (1–2°C). The first barophilic organisms were isolated in 1979 by Yayanos and they could tolerate 40 MPa. These barophiles are polyextremophilic in nature, because they are often psychrophilic and barophilic. The cultured diversity of a barophile is usually isolated from 100 to 40 MPa and at 2–5°C temperature. Some barosensitive cultured isolates isolated from deep oceans include *Vibrio marinus*, *Shewanella* sp. PT99*, Shewanella benthica, Colawellia* spp. and *S. hanedai* DSK1. Barophiles are also found below 2000 m depth. At Marina Trench, challengers isolated the organisms from 10,898 m depth, where the pressure was 1100 atm and temperature 2°C. Hence, this revealed that it is difficult to set a high pressure limit known for barophiles. The main surprising characteristic for isolation of a barophile is that the condition must be dark, because in the ocean at high pressure, low temperature and dark conditions prevail. Hence barophiles are sensitive to UV light and gamma radiation; however, it is as yet unclear whether barophiles have DNA repair enzymes or not (Horikoshi, 1998b).

Barophiles are grown fast at high pressure; if low pressure is provided to them, it leads to membrane fragmentation, nucleotide structure modification and plasmolysis. In the strain of *Microcyclus aquaticus*, it was observed that killing of the cell occurred by decompression. It might be assumed that the cell did not produce gas vacuoles at low pressure for survival that could hold the cell growth at insufficient pressure and temperature. Motility is the main factor which was affected at low pressure; in flagella, the motor is tightly coupled and depends on proton power, but when organisms are affected by low pressure, protonation and deprotonation occurs, so the cell decreases movement for survival.

Membrane fluidity is also affected, in lipid moieties of the membrane whereby the acyl chain is increased and membrane gelation occurs. This is referred to as hemoviscous adaptation in which bacteria increases the number of polyunsaturated fatty acids over mono-unsaturated fatty acids for survival strategy. At high pressures the substrate transport system performs very well compared to low pressure. In the context of cell division, the cell grows in a long filamentous form and long lag phase at high pressure, and decreases cell division and changes the cell morphology at low pressure. DNA replication is also affected at low pressure and high temperature, leading to modification in nucleotide formation and subsequently the cells can't survive (Barlett, 1992). Because of limited research on barophiles, the applications are also limited, but the enzymes from these organisms are used as cryoprotectants; they are also used in food preservation at very low temperatures, and in molecular research and the medical/ pharmaceutical fields.

74.2.6 Radiophiles

Organisms with extraordinary DNA damage resistance to the lethal mutagenic ionization and UV radiation, are termed as radiophiles. Very scanty knowledge is reported for radiophiles; to date only one organism has been reported viz., *Deinococcus* spp. The first strain of *Deinococcus radiodurans* was reported in 1965 by Anderson from sterilized X-ray cans. This bacterium had a red-pigment colony, and was non-sporulated and Gram-positive. Other species of *Deinococcus* are reported such as *Deinococcus radiophilus*, *Deinococcus proteolyticus, Deinococcus radiopugnans* and *Deinobacter grandis*. In *Deinococcus radiodurans*, two types of repair mechanism exist, one is excision repair and the second one is recombination repair of DNA. Recently the DNA polymerase from *Deinococcus radiodurans* were identified on the protein level, and are of similar homology with polymerase I of *E. coli*. The structure of the enzyme is similar in this bacterium but the resistance at molecular level is broadly different between them (Minton, 1994). The radiation resistant to carotenoid pigment was isolated from *Deinococcus radiodurans*, which could lead to highly applicable aspects in biotechnology (Laurant Lemee, 1996).

74.2.7 Xerophiles

While water requirement is undoubtedly important for all life forms, some organisms which grow in conditions of extreme desiccation are called the xerophilic microbial community. The survival strategies for xerophilic organisms include that the metabolic activities enter into a dormancy stage or anhydrobiosis. When organisms are in an anhydrobiosis state, they can survive high radiation, pressure and temperature up to 151°C. Nematodes, Microbes, *Artemiasalina*, Fungi, mold (*Wallemia sebi)* and lichens are included in xerophilic life forms (Jasani, 2015). Xerophiles increase the salinity of the habitat, and thus increase the colonization of halophilic organisms with unique properties (Rewald, 2012).

74.2.8 Capnophiles

Organisms grown in an atmosphere of high CO_2 are called capnophilic; they are very diverse phylogenetically, have various metabolic potentials and varying evolutionary relationships from eachother. Capnophiles are isolated from plants, wastewater, animal rumens and mammalian cavities where CO_2 content is sufficient for survival. Scientific interest was given to these types of bacteria because they cause food spoilage, but also for disease studies. Capnophiles use CO_2 for fermentation, amino acid synthesis and acetyl-CoA production (Eugenio-Felipe, 2015). Capnophilic strains are used for waste water treatment because of their unique survival properties in not requiring O_2. They can be applied for disease treatment and the anaerobic fermentation industry. The main use of capnophiles includes organic acid production such as succinic acid (Joeri, 2010). (See Table 74.10.)

74.2.9 Oligotrophs

Oligotrophs grow in low amounts of nutrients or in the absence of nutrients; the organisms forage minerals from the outer environment. They are also called oligocarbotrophs, because the bacteria use trace amounts of organic carbon. On the basis of nutrient requirements, oligotrophs are divided to two parts: oligocarbotrophs and oligonitrotrophs. Nowadays terminology extends to oligoferrotrophs and oligophosphotrophs. Obligate and facultative types of organisms are included in this type. The organisms that grow in nutrient rich conditions are called copiotroph; this term was first coined by Poindexter (1981). Oligotrophs do not include specific genera or groups of bacteria. The saprophytic substratum, wood decomposition material, low nutrient-containing soil, sea water, sediments, these all are common habitats for oligotrophs, where carbon and nitrogen sources are available. In the marine ecosystem the pelagic zone is low in nutrition, where carbon sources are available; these carbon materials are photo-assimilated by phytoplanktonic cells. Some fungi and bacteria grow under low nutrient conditions such as *Fusarium aquaeductum, Saccharomyces cerevisae, Pseudomonas fluorescens, P. aeruginosa, Penicillium lilacinum, Aspergillus fumigates, A. glaucus, Scopulariopsis repens, Aureobasidium pullulans* and *Cladosporium* spp. These are commonly found in oligotrophic conditions, but the fungal diversity is more dominant over the bacterial diversity; the reason behind this might be that the bacterial cell growth cycle is not so long as fungi. Fungi generally survive in all types of conditions over a long period of time (Wainwright, 1993).

Table 74.10 Example of capnophilic species from varied sources.

Name of organisms	Source of isolation
Streptococcus pneumoniae *Streptococcus thoraltensis* *Haemophilus influenzae*	Human patients and pigs (Devriese, 1997)
Streptococcus equi **subsp.** *equi*	Lymph nodes of sick horses South Korea (Moon, 2015)
Helicobacter pylori	Sample of gastric biopsies (Guillerm, 2016)
Lactobacillus **strain**	Crystal Geyser (Eugenio-Felipe, 2015)
Porphyromonas gingivalis, *Prevotella intermedia*, *Fusobacterium nucleatum*, *Bacteroides forsythus*	Sample of subgingival biofilm (Surada, 2013)

- The physiology of oligotrophs is unique compared to other types of extremophiles; bacteria scavenge the nutrients from outer environments in the form of gases, solutions or volatile substances.
- The oligotrophs have a multi-response strategy for substrate uptake and utilization; at one time they can utilize more than one source of trace elements from the environment.
- Oligotrophs can grow in distilled water, as reported by Bigger and Havelock Nelson (1943).
- Antibiotic resistance in *Pseudomonas* spp. was found from mineral water in Germany. If oligotrophs were constantly exposed to the environment without nutrient availability, it altered its structural physiology and

developed resistance towards a specific substrate (Rosenberg, 1989).

- Oligotrophs are significant bio-deterioration agents in ecology. Oligotrophs are generally applied in the medical field for antibiotic preparation, and enzyme production.
- In the ecosystem oligotrophs function in the recycling of nutrients, such as carbon, nitrogen, ferrous and phosphorous, because of unique scavenging characteristics.
- The extremely oligotrophic bacterium *Rhodococcus erythropolis* N9T-4, was isolated from a crude oil contaminated site, so that these types of bacteria might be used as significant environmental cleaners with less nutrient requirements and to be industrially applicable as a unique biological product (Ohhata, 2007).

74.3 Concluding Remarks

Thus, overall, the marine environment can be defined as a highly potent source for extremophile prospection and subsequent biotechnological applications. In particular, the newer developments in molecular techniques will help enhance the extremophile data consisting of unique metabolic and genetic capabilities.

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Chapter 74

Marine Extremophiles

Adaptations and Biotechnological Applications

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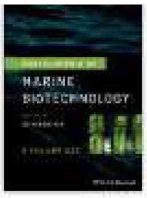
Summary

Extreme environments are also considered as highly fluctuating in physical conditions like temperature, pH, pressure, nutrient availability, radiation, salinity, etc. However, several microorganisms both eukaryotes and prokaryotes, are known to survive these conditions and such organisms are called as extremophiles. For the adaptation in extreme environments, many organisms have developed unique characteristics. These adaptive strategies are considerably important in various significant biotechnological applications. This chapter discusses different types of extremophile and their adaptations. It includes hyperthermophile, thermophile, mesophile, psychrophile, acidophile, alkalophile, halophile, barophile, radiophile, xerophile, capnophile, and oligotrophile. Thus, overall, the marine environment can be defined as a highly potent source for extremophile prospection and subsequent biotechnological applications. In particular, the newer developments in molecular techniques will help enhance the extremophile data consisting of unique metabolic and genetic capabilities.



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