Life in Extreme Environments: The Universe May Be More Habitable Than We Thought

Artist's concept of an astronaut examining a rock sample on Mars. Life has been found living inside rocks in the various extreme environments on Earth. Clues derived from finding life in such terrestrial locations will serve as a guide to understanding where we might find life on other worlds.

Clearly there are physical and chemical extremes that should make life based on organic carbon difficult if not impossible. Yet, within the last few decades we have found organisms that have punctured these seemingly insurmountable limits and have come to called "extremophiles" from the Latin "extremus" (being on the outside) and the Greek "philos" for love. Organisms that can live in more than one extreme, for example *Sulfalobus acidocaldarius* (a member of the Archea - an ancient branch off the family tree of life) lives at pH 3 and 80°C, are called polyextremophiles.

Who are the extremophiles?

The word "Extremophile" often invokes images of microbes, and so-called "simple" ones at that, yet the taxonomic range spans all three domains. (Note that life itself is so complex that the human creation of life has remained elusive. Thus, it is unjustifiably arrogant of us to call any form of life "simple".) While all organisms that live at extremely high temperatures are Archaea or Bacteria, eukaryotes (organisms whose cells have nuclei) are common among organisms that thrive at low temperature, extremes of pH (high acidity or alkalinity) pressure, water, and salt levels. Extremophiles include multicellular organisms, cold-lovers include vertebrates such as penguins and polar bears.

To qualify as an extremophile, does an organism have to be an extremophile during all life stages? Under all conditions? Not at all. Spores, seeds, and sometimes eggs or larval stages are all far more resistant to environmental extremes than adult forms. Yet some adult organisms - trees, frogs, insects, and fish - can endure remarkably low temperatures during the winter as a result of seasonal shifts in physiology such as hibernation.

A Scanning Electron Micrograph of a Tartigrade

One of the most resilient organisms known are tardigrades ("water bears"). Tardigrades can go into a hibernation mode - called the tun state - one that is more akin to "suspended animation" whereby it can survive temperatures from -253°C to 151°C, as well as exposure to x-rays, and vacuum conditions. When you place tardigrades in perfluorocarbon fluid (again while hibernating), at a pressure of 600 MPa, (that's almost 6,000 times atmospheric pressure at sea level) they emerge from the experience just fine . Even the bacterium *Deinococcus radiodurans*, the most radiation resistant organism known, only achieves this resistance under some conditions such as fast growth and in nutrient-rich medium.

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Classification and examples of extremophiles

Environmental parameter	type	Definition	examples
temperature	hyperthermophile thermophile mesophile psychrophile	growth >80°C growth 60-80°C 15-60°C <15°C	*Pyrolobus fumarii*, 113°C *Synechococcus lividis* *Homo sapiens* *Psychrobacter*, some insects
radiation			*Deinococcus radiodurans*
pressure	barophile piezophile	Weight loving Pressure loving	unknown For microbe, 130 MPa
vacuum		tolerates vacuum (space devoid of matter)	tardigrades, insects, microbes, seeds.
desiccation	xerophiles	Anhydrobiotic	*Artemia salina*; nematodes, microbes, fungi, lichens
salinity	halophile	Salt loving	*Halobacteriacea, Dunaliella salina*
pH	alkaliphile acidophile	pH >9 low pH loving	*Natronobacterium, Bacillus firmus* OF4, *Spirulina spp.* (all pH 10.5) *Cyanidium caldarium*, *Ferroplasma sp.* (both pH 0)
oxygen tension	anaerobe microaerophil aerobe	cannot tolerate O_2 tolerates some O_2 requires O_2	*Methanococcus jannaschii* *Clostridium* *Homo sapiens*
chemical extremes	gases metals	Can tolerate high concentrations of metal (metalotolerant)	*Cyanidium caldarium* (pure CO_2) *Ferroplasma acidarmanus*(Cu, As, Cd, Zn); *Ralstonia* sp. CH34 (Zn, Co, Cd, Hg, Pb)

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Life in Extreme Environments

Dry environments

Imagine a desert and a feeling of dehydration follows. In the absence of water, lipids (fats) , proteins and nucleic acids (DNA, RNA) suffer structural damage. The Atacama desert located on the high northern Andean plains of Chile is one of the oldest, driest hot deserts on the Earth, while the Antarctic dry valleys are the coldest, driest places on Earth. In both cases, despite environmental extremes, life exists in the form of microbes: cyanobacteria, algae, lichens, and fungi.

Anhydrobiosis is a strategy organisms use to survive dry spells. During anhydrobiosis their cells come to contain only minimal amounts of water. No metabolic activity is performed. A variety of organisms can become anhydrobiotic, including bacteria, yeast, fungi, plants, insects, the aforementioned tardigrades, mycophagous (fungi-eating) nematodes, and the brine shrimp *Artemia salina* (also known as "Sea Monkeys" when marketed to school age children). During the drying out process (desiccation), less available water forces substances to increase in their concentration. Such increases lead to stressful responses within a cell that are similar to those of a cell experiences when exposed to high salt environments.

The ultimate dry environment is the "desert" of space. Adaptations to desiccation are critical for organisms to survive in interplanetary space. One organism in particular (described below) is a natural born space traveler.

Salinity

As airplanes descend into the San Francisco area, red patches on the eastern shore of the South Bay are conspicuous. These are evaporation ponds of Cargill Salt Company. The cause of the red color is halophilic (salt-loving) microbes that produce red pigments called carotenoids. The microbes involved are either members of the Archaea, a major group of microbes superficially similar to bacteria, or the green alga Dunaliella salina. At a bit lower (25-33%) salinity, bacteria, cyanobacteria, other green algae, diatoms and protozoa are found. Some Archaea, cyanobacteria, and *Dunaliella salina* can even survive periods in saturated sodium chloride - about as salty an environment as one can imagine.

Salt water can evaporate leaving deposits ("evaporite deposits") consisting of salts such as sodium chloride (halite) and calcium sulfate (gypsum). Within evaporates are fluid inclusions - small trapped pockets of water - which can provide a refuge for microbes for at least six months. Our research group showed that cyanobacteria trapped within dry evaporite crusts can continue to have low levels of metabolic function such as photosynthesis. These deposits also form nice fossils of the organisms trapped within. Although highly controversial, others claim that bacteria might survive for millions of years in the fluid inclusions of salt deposits including evaporates. Tantalizingly, such deposits have been found on Mars.

So how do cells adapt to this potentially deadly environment? To prevent an exodus of water from the cell, halophiles offset the high salt in the environment by accumulating such compounds as potassium and glycine-betaine. This allows a balance of salts inside and outside of the cell preventing water from flowing outward as would be the case if lower salt levels existed within the cells.

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Acidity and Alkalinity

Yellowstone National Park has bubbling acid hotsprings that would make a witch's cauldron seem benign. They also teem with life. Once again we have been astounded that such environments harbor life.

Acidity and alkalinity are measures of the concentration of protons, the units used are pH units. The lower the number (down to zero), the higher the acidity. The higher (up to 14), the more alkaline. A neutral pH near 7 is optimal for many biological processes, although some - such as the light reactions of photosynthesis - depend on pH gradients. In nature, pH can be high, such as in soda lakes or drying ponds, or as low as 0 and below. Organisms that live at either extreme do this by maintaining the near-neutral pH of their cytoplasm (i.e.) the liquid and materials within their cells.

Low pH is the realm of acidophiles - "acid lovers". If you are looking for champion acid lovers, forget fish and cyanobacteria which have not been found below pH 4, or even plants and insects which don't survive below pH 2 to 3. The extreme acidophiles are microbes. Several algae, such as the unicellular red alga *Cyanidium caldarium* and the green alga *Dunaliella acidophila*, are exceptional acidophiles both of which can live below pH 1. Three fungi, *Acontium cylatium, Cephalosporium sp.,* and *Trichosporon cerebriae*, grow near pH 0. Another species, *Ferroplasma acidarmanus*, has been found growing at pH 0 in acid mine drainage in Iron Mountain in California. These polyextremophiles (tolerant to multiple environmental extremes) thrive in a brew of sulfuric acid and high levels of copper, arsenic, cadmium, and zinc with only a cell membrane and no cell wall.

High Temperature

Temperature is a critical parameter because it determines whether liquid water is present. If temperature is too low, enzymatic activity slows, membrane fluidity decreases. Below freezing ice crystals form that slice through cell membranes. High temperatures can irreversibly alter the structure of biomolecules such as proteins, and increase membrane fluidity. The solubility of gasses in water is correlated with temperature, creating problems at high temperature for aquatic organisms requiring oxygen or carbon dioxide.

Octopus Spring, an alkaline (pH 8.8Ð8.3) hotspring in Yellowstone National Park, USA, is situated several miles north of Old Faithful geyser. The water flows from the source at 95°C to an outflow channel, where it cools to a low of 83°C. About every 4Ð5 minutes a pulse of water surges from the source raising the temperature as high as 88°C. In this environment the pink filamentous *Thermocrinis ruber* thrives.

As it happens, organisms can outwit theory. Geysers, hotsprings, fumaroles and hydrothermal vents all house organisms living at or above the boiling point of water. The most hyperthermophilic (VERY hot loving) organisms are Archaea, with *Pyrolobus fumarii* (of the Crenarchaeota), a nitrate-reducing chemolithotroph (an organism that derives energy from minerals), capable of growing at up to 113°C, is the current champion. As such, these hyperthermophiles are able to prevent the denaturation and chemical modification (breakdown) of DNA which normally occurs at or around a comparatively cool 70°C. The stability of nucleic acids is enhanced by the presence of salts which protect the DNA from being destroyed.

Thermophily (living in hot places) is more common than living in scalding, ultra hot locales, and includes phototrophic bacteria (i.e., cyanobacteria, and purple and green bacteria who derive energy from photosynthesis), eubacteria (i.e., *Bacillus, Clostridium, Thiobacillus, Desulfotomaculum, Thermus,* lactic acid bacteria, *actinomycetes, spirochetes,* and numerous other genera), and the Archaea (i.e., *Pyrococcus, Thermococcus, Thermoplasma, Sulfolobus,* and the methanogens). In contrast, the upper limit for eukaryotes is ~ 60°C, a temperature suitable for some protozoa, algae, and fungi. The maximum temperature for mosses is another 10° lower, vascular plants (house plants, trees) about 48°C, and fish 40°C.

Low Temperature

Representatives of all major forms of life inhabit temperatures just below 0°C. Think winter, think polar waters. While sperm banks and bacterial culture collections rely on the preservation of live samples in liquid nitrogen at -196°C, the lowest recorded temperature for active microbial communities and animals is substantially higher at -18°C.

Freezing of water located within a cell is almost invariably lethal. The only exception to this rule known from nature is the nematode *Panagrolaimus davidi* which can withstand freezing of all of its body water. In contrast, freezing of extracellular water - water outside of cells - is a survival strategy used by a small number of frogs, turtles and one snake to protect their cells during the winter. Survival of freezing must include mechanisms to survive thawing, such as the production of special proteins or "cryoprotectants" (additives that protect against the cold) called "antifreeze" proteins. The other method to survive freezing temperatures is to avoid freezing in the first place. Again "antifreeze" molecules are produced which can lower the freezing point of water 9 to 18°C. Fish in Antarctic seas manage to employ these mechanisms to their advantage.

Other changes with low temperature include changes in the structure of a cell's proteins - most notably their enzymes - so as to allow them to function at lower temperatures. The fluidity of cell membranes decreases with temperature. In response, organisms that are able to adapt to cold environments simply increase the ratio of unsaturated to saturated fatty acids thus retaining the required flexibility of membranes.

Radiation

Radiation is a hazard even on a comfortable planet like Earth. Sunlight can cause major damage unless mechanisms are in place to repair - or at least limit - the damage. Humans lacking the capacity to repair ultraviolet (UV) damage have xeroderma pigmentosa. This disease is so serious that suffers cannot leave their house during the day unless completely covered, and must even shade the windows in their homes.

Once you leave the protected surface of Earth, things can get more hostile. One of the major problems that organisms might face during interplanetary transfer (inside a rock blasted off of a planet by a large impact event for example), living on Mars, or even at high altitudes on Earth is the high levels of UV (ultraviolet) radiation.

"A "tetrad" of *Deinococcus radiodurans* cells.

In space there is cosmic and galactic radiation to contend with as well. The dangers of UV and ionizing radiation range from inhibition of photosynthesis up to damage to nucleic acids. Direct damage to DNA or indirect damage through the production of reactive oxygen molecules creates can alter the sequence or even break DNA strands.

Several bacteria including two Rubrobacter species and the green alga *Dunaliella bardawil*, can endure high levels of radiation. *Deinococcus radiodurans*, on the other hand is a champ and can withstand up to 20 kGy of gamma radiation up to 1,000 joules per s02. meter of UV radiation. Indeed, *D. radiodurans* can be exposed to levels of radiation that blow its genome into pieces only to have the organism repair its genome and be back to normal operations in a day.

This extraordinary tolerance is accomplished through a unique repair mechanism which involves reassembling damaged (fragmented) DNA. Scientists at the Department of Energy are looking to augment *D. radiodurans* genome such that it can be used to clean up mixed toxic and radioactive spills. So eager are

biotechnologist to understand just how *D. radiodurans* does what it does that its genome was among the first organisms to be fully sequenced.

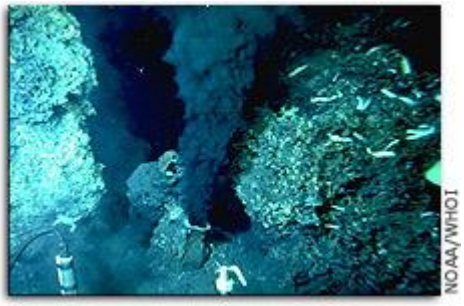
Gravity

Gravity is a constant force in our lives; who has not imagined what it would be like to be an astronaut escaping gravity even temporarily? The universe offers a variety of gravitational experiences, from the near absence of gravity's effects in space (more accurately referred to as microgravity) to the oppressive gravitational regimes of planets substantially larger than ours.

Gravitational effects are more pronounced as the mass of an organism increases. That being said, flight experiments have revealed that even individual cells respond to changes in gravity. Cell cultures carried aboard various spacecraft including kidney cells and white blood cells showed marked alterations in their behavior, some of which is directly due to the absence of the effects of a strong gravity field. Indeed, recent work conducted aboard Space Shuttle missions has shown that there is a genetic component (as yet understood) to kidney cell responses to microgravity exposure.

Pressure

Pressure increases with depth, be it in a water column or in rock. Hydrostatic (water) pressure increases at a rate of about one-tenth of an atmosphere per meter depth, whereas lithostatic (rock) pressure increases at about twice that rate. Pressure decreases with altitude, so that by 10 km above sea level atmospheric pressure is almost a quarter of that at sea level.



A deep ocean hydrothermal vent belching sulfide-rich hot water. The black "smoke" is created as sulfide minerals form in the mixing process between vent water and colder ocean water. These minerals settle and can accumulate to great thicknesses.

The boiling point of water increases with pressure, so water at the bottom of the ocean remains liquid at 400¡C. Because liquid water normally does not occur above ~100°C, increased pressure should increase the optimal temperature for microbial growth, but surprisingly pressure only extends temperature range by a few degrees suggesting that it is temperature itself that is the limiting factor.

The Marianas trench is the world's deepest sea floor at 10,898 m, yet it harbors organisms that can grow at temperature and pressure we experience everyday. It has also yielded obligately piezophilic species (i.e. organisms that are pressure loving and can only grow under high pressure) that can only grow at the immense pressures found at the ocean's greatest depths.

Other extreme conditions

A bit of creative thinking suggests other physical and chemical extremes not considered here, including unusual atmospheric compositions, redox potential, toxic or xenobiotic (manmade) compounds, and heavy metal concentration. There are even organisms such as *Geobacter metallireducens* that can survive immersion in high levels of organic solvents such as those found in toxic waste dumps. Others thrive inside the cooling water within nuclear reactors. While these organisms have received relatively little attention from the extremophile community, the search for life elsewhere may well rely on a better understanding of these extremes.

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