MICROBIAL BIOTECHNOLOGY

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Lecture-11

Lec 11: Physiology of Extremophiles and adaptation- energy storage, temperature, pH and pressure.

Hello friends, welcome to my course on microbial biotechnology. We are in module 3, which deals with the physiology of microorganisms and their adaptation to the environment. In this lecture, we will discuss the physiology of extremophiles and their adaptation, and then explore certain concepts like energy storage, temperature, pH, and pressure conditions under which these extremophiles survive. So, briefly, we will discuss energy storage, as I mentioned, the types of different extreme environments microorganisms live in or face, and the effect of environmental factors on microbial growth, adaptation to variable temperature, pH, and pressure. Let us start with the energy storage strategies and adaptation mechanisms in microorganisms.

Humans, particularly those living in very difficult environments like the high Himalayas or other areas where there is only a seasonal supply of food materials, have long been known to store food to cope with the scarcity of food in the lean season. This is an overall strategy actually employed by many higher organisms. Microorganisms have also evolved mechanisms to store energy-rich compounds during periods of nutrient abundance, allowing them to survive times of nutrient scarcity. Mechanisms to store energy-rich compounds during periods of nutrient abundance allow them to survive times of nutrient scarcity.

These storage strategies highlight the metabolic flexibility and resilience of microorganisms, enabling them to thrive in diverse and fluctuating environments. Microorganisms synthesize and accumulate a variety of storage compounds that serve as carbon, energy, and phosphate sources. Some of these key storage compounds we will discuss in this lecture today include storage carbohydrates, energy-rich lipids, inorganic reserves, and several others like trehalose. Let's start with the storage carbohydrates and

how microbes store these for their future use. Let's start with glycogen, which is a polysaccharide made of glucose units.

It serves as a primary carbon and energy reserve in many bacteria, fungi, and even in animals. When nutrients are scarce, glycogen is broken down to release glucose for energy production. Then there is starch, which is primarily found in plants and some algae. Starch is a polysaccharide composed of glucose units. It serves as a long-term energy reserve and can be hydrolyzed into glucose when needed.

Then there are energy-rich lipids like poly-beta-hydroxybutyrate or PHB, which is a biopolymer that bacteria store. PHB is an important carbon and energy reserve. It is particularly prevalent in bacteria like Rhodobacter and Bacillus, but it is not found in eukaryotes. It serves as a reservoir for carbon, especially when external carbon sources are limited. Then we have neutral lipids in filamentous fungi and yeast.

They often store triglycerides within their vacuoles. These neutral lipids provide an energy source that can be mobilized during nutrient shortages or environmental stress. Then, microbes also store inorganic material or inorganic compounds. For example, volutin granules. These are the phosphate granules.

These are found in both prokaryotes and eukaryotes. Volutin granules are composed of polyphosphates and serve as a phosphate and energy reserve. These reserves are crucial for essential metabolic processes like nucleotide synthesis, cell division, and ATP generation. Then we have sulfur granules in sulfur bacteria like Thiobacillus. They store sulfur granules by oxidizing hydrogen sulfide.

When external sulfur sources are exhausted, these granules are oxidized to sulfate, providing reducing equivalents for critical metabolic processes such as carbon dioxide fixation and oxidative phosphorylation. Then there are other compounds like trehalose, which is a disaccharide synthesized by filamentous fungi, yeast, and some bacteria. It plays a key role as a protective agent during environmental stress conditions like desiccation, heat shock, or freezing. Trehalose stabilizes cellular structures and prevents damage by forming protective glasses around proteins and membranes, and it's a very important molecule for survival under harsh conditions. So hydrolysis of these storage reserves, how these stored compounds are finally utilized in times of need.

The breakdown of these energy reserves is facilitated by enzymes like phosphorylases, which catalyze the hydrolysis of polysaccharides like glycogen and starch to release

glucose 1-phosphate. This glucose can then enter various catabolic pathways such as glycolysis or the pentose phosphate pathway to produce ATP and support the microorganism's energy needs during periods of nutrient scarcity. Now let us look into the details of the survival of microorganisms in extreme environments. Extreme environments like acidic hot springs, saline and alkaline lakes, deserts, and ocean beds exist in nature and are inhospitable habitats for conventional life forms like us or even plants. These environments can be characterized as conditions that surpass the normal acceptable range, thus qualifying as extreme conditions.

Remarkably, certain microbes are capable of thriving and proliferating in such harsh settings. These organisms not only endure specific extreme conditions but often depend on them for their survival and growth. Extremophiles, as they are called, which survive in such harsh settings, are predominantly found within the microbial realm, demonstrating a remarkable ability to tolerate a wide range of environmental extremes, surpassing that of other life forms. So these are environmental niches in which other organisms can barely survive.

So as already discussed, when we talk about extreme environments, it is not just of one type. The sea ice, permafrost and polar regions, cold seeps and the mud volcanoes, shallow water hydrothermal vents, hot springs, and then hyper acidic lakes and volcanoes, deserts and arid environments with almost no water, and then the acid mine drainage. And then the deep sea anoxic lakes, deep sea hydrothermal vents, then serpentinizing environments, then deep sea sediment trenches, marine and continental subsurfaces. Then deep sea sediment trenches, marine and continental subsurfaces.

We have soda lakes and hypersaline lakes. Then nuclear contaminated sites which may be natural or man-made. Then we have ophiolites and continental serpentinization. So these are the types of extreme environments where we can find various microbes surviving by adaptations. So these kinds of microbes we call extremophiles because they can survive in extreme environments, and can be simply named as acidophiles, alkaliphiles, piezophiles, halophiles, xerophiles, radiophiles, metallophiles, thermophiles

and psychrophiles. We will be discussing some of these today and in the next lecture. So, how do environmental factors affect microbial growth? This is an important point to ponder before we go into the detailed discussion. We have seen that microorganisms can withstand and survive in extreme environmental conditions. They are the only ones that can be present in such habitats, which are otherwise inhospitable to other organisms.

And for them, this is a normal habitat. But for these, the microbes need to adapt and respond to changes within their habitats to survive. Ecological distribution and understanding the impact of environmental microbes will help us comprehend the survival strategies in such extreme environmental conditions. So, adaptations to various conditions—a microbe may be under stress, environmental stress, due to which the DNA may be damaged, the protein may be damaged, and then the reactive oxygen species effect will be there. How they adapt to these kinds of environmental challenges is what we are trying to understand in this lecture.

So, for these, they have evolved various mechanisms to manage the specific stresses they encounter. There is not just one kind of challenge, and so there are also similarly multiple kinds of strategies to manage these kinds of stresses. The microorganisms adjust their biochemical pathways and structural components to maintain functionality and stability under extreme conditions, such as high temperature, pressure, or salinity. So, for example, if such stresses cause DNA damage or protein damage, the microorganism will try to evolve mechanisms that will safeguard the DNA and the protein. Such adaptations involve changes in enzyme activity, membrane composition, and osmotic regulation to ensure survival and proper cellular function in harsh conditions.

Adaptation to variable temperature. Earth's surface temperature ranges from almost minus 100 degrees in East Antarctica to 495 degrees centigrade in the deep-sea hydrothermal vents. In geothermal or magmatic environments, temperature can exceed 100 degrees due to high pressure. The highest surface temperature recorded is about 71 degrees centigrade in Iran's Lut Desert, which is on the surface. Microbial life can survive from minus 25 to 130 degrees centigrade, with metabolic activity ranging between minus 20 to 122 degrees centigrade as reported today.

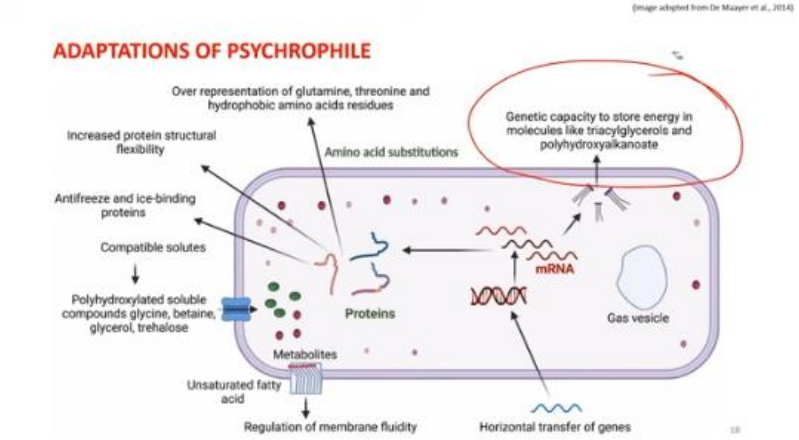
Now, what is the effect of temperature? So, if you look at the growth rate as the temperature increases, the growth will be more and then reach an optimum value, and suddenly it will start declining. So, temperature greatly affects microorganisms as they lack the ability to control their internal temperature. Enzyme-catalyzed reactions essential for growth are particularly influenced by temperature. Each enzyme has an optimal temperature at which its function is best or optimum.

So, cold environments or the psychrophiles, more than 80% of Earth's biosphere is permanently below 5 degrees centigrade, and diverse microorganisms have been discovered in these seemingly inhospitable regions worldwide. The ability of organisms to

survive at low temperatures is determined by the freezing point of water inside the cells. Crystallization of the intracellular water is lethal for most organisms. It will rupture the cell except for the nematode, Panagrolaimus davidi, which can survive the freezing of all the body water. It will rupture the cell except for the nematode, Panagrolaimus davidi, which can survive the freezing of all the body water.

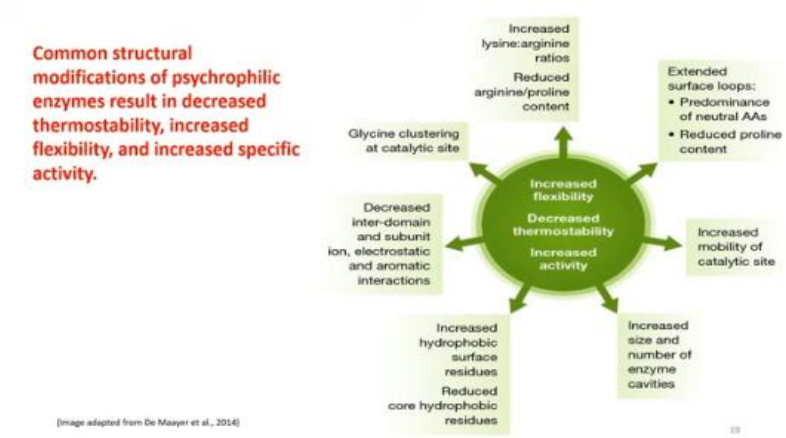
Psychrophilic species such as Shewanella, Vibrio, Micrococcus, Methanogenium, and Bacillus have been identified. The genus Moritella consists exclusively of psychrophiles. Archaea, cold-living organisms that inhabit temperatures below 15 degrees centigrade, have adapted to the challenges of low temperature and high viscosity in aqueous environments. So these are some examples of psychrophiles. You can see the snow surface with snow algae here in this picture and the lichen here, Xanthoria.

These continue to photosynthesize at minus 24 degrees centigrade. So how do psychrophiles adapt? There are various mechanisms, like at the genetic level, there may be horizontal gene transfer, acquiring fitness genes which help them adapt to such conditions. Then there is a genetic capacity to store energy in molecules like triacylglycerols and polyhydroxyalkanoate, which helps meet their energy demands at a later point in time. Then there is the regulation of membrane fluidity, which will not allow the entry and exit of metabolites but rather control and regulate it.



Other strategies include amino acid substitutions, such as the overrepresentation of glutamine, threonine, and hydrophobic amino acid residues. Then there is increased protein structural flexibility. Very interestingly, they have antifreeze and ice-binding proteins which help protect the organism as a whole. And then there is the deployment of compatible solutes and polyhydroxylated soluble compounds like glycerol, betaine, and trehalose.

Some of the common structural modifications of psychrophilic enzymes result in decreased thermostability, increased flexibility, and increased specific activity.



So this increased flexibility, decreased thermostability, and increased activity. So here the lysine-arginine ratios are increased. Arginine-proline and proline content are reduced. And then there is glycine clustering at the catalytic site. Decreased interdomain and subunit ion electrostatic and aromatic interactions occur.

Increased hydrophobic surface residues, reduced core hydrophobic residues, and increased size and number of enzyme cavities occur. Extended surface loops, predominance of neutral amino acids, reduced proline content, and increased mobility of the catalytic site. So these are some of the common structural modifications of enzymes in psychrophiles, which help in increased flexibility, decreased thermal stability, and increased specific activity. Now let us look into the other extreme: warm temperatures. Such organisms that survive in higher temperatures are known as thermophiles.

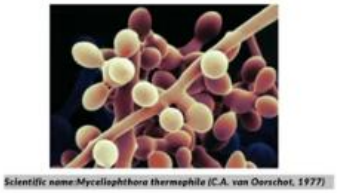
Around 25 to 40 degree centigrade, they survive and exhibit growth rates at temperatures exceeding 45 degree centigrade. Various extreme environments, both terrestrial and submarine, harbor high-temperature conditions suitable for the growth of thermophiles. These habitats encompass thermal vents, hot springs, and boiling steam vents, while surface soil and compost piles also provide suitable environments. Thermophiles can be categorized into two groups. Facultative thermophiles, which are capable of thriving at both high and moderate temperatures, and obligate thermophiles, which require high temperatures for growth.

WARM TEMPERATURE: THERMOPHILES

Thermophiles thrive at temperatures above 25–40°C, exhibit maximum growth rates at temperatures exceeding 45°C. Various extreme environments, both terrestrial and submarine, harbor high-temperature conditions suitable for the growth of thermophiles. These habitats encompass thermal vents, hot springs, and boiling steam vents, while surface soil and compost piles also provide suitable environments. Thermophiles can be categorized into two groups: **facultative thermophiles**, capable of thriving at both high and moderate temperatures, and **obligate thermophiles**, which require high temperatures for growth.

Some examples of thermophiles are Methanosarcina thermophila, Methanobacterium wolfei, Methanobacterium thermoautotrophicum, Archaeglobus profundus, Alicyclobacillus acidoterrestris, and Alicyclobacillus acidocaidarius. How do adaptations to higher temperatures occur? One of the strategies employed is having a smaller genome size. Genes for polyamine biosynthesis, priA helicase, DNA-binding protein HU, heat shock proteins, GrpE, DnaK, DnaJ, GroEL, co-chaperones, GroES, heat-inducible transcription repressors, and cold-shock proteins from the Csp family are deployed. GrpE, DnaK, DnaJ, GroEL, co-chaperones, GroES, heat-inducible transcription repressors, and cold-shock proteins from the Csp family are deployed.

Examples of Thermophiles



Scientific name:Mycelisphthora thermophila (C.A. van Oorschot, 1977)

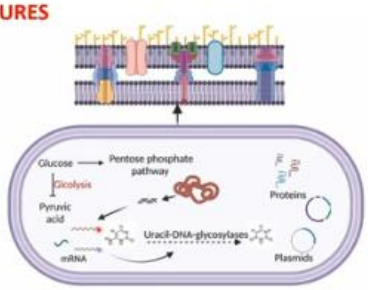
Some of the common examples include

- *Methanosarcina thermophila*
- *Methanobacterium wolfei*
- *Methanobacterium thermoautotrophicum*
- *Archaeglobus profundus*
- *Alicyclobacillus acidoterrestris*
- *A. acidocaidarius*

https://www.biologyonline.com/dictionary/thermophile

ADAPTATIONS TO HIGHER TEMPERATURES

1. Small genome size.
2. Genes for polyamine biosynthesis, PriA helicase, DNA-binding protein HU, heat shock proteins (GrpE, Dnak, DnaJ, GroEL), co-chaperone GroES, heat-inducible transcription repressors, and cold shock protein from the Csp family.



(Image adopted from Salwan & Sharma, 2022)

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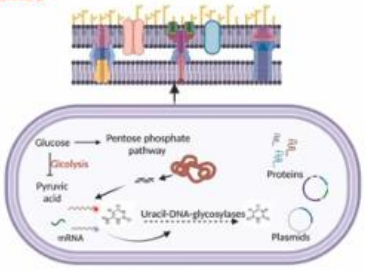

(Image adopted from Salwan & Sharma, 2022)

This helps in the adaptation to higher temperatures. There are preferences for G and A in the first and third codon positions, and over-represented amino acids like I, V, Y, W, R, E, and L. The presence of diverse insertion sequence elements, the pentose phosphate pathway favored at high temperatures over glycolysis, and the glycosylation of carotenoids aid in thermophilic adaptation. There is an absence of the uracil DNA glycosylase gene, which is linked to cytosine deamination. Heat-shock proteins.

Thermophiles produce HSPs or heat-shock proteins and chaperones that assist in protein folding, especially under high-temperature stress. HSPs are activated in response to heat shock and are classified based on their molecular mass, for example, HSP 70 and HSP 60. These chaperones help fold nascent or unfolded polypeptides and prevent protein aggregation. The well-studied Hsp60-chaperonin complex, or the GroEL-GroES in bacteria, plays a key role in protein folding by creating a protected environment for proteins to fold properly. If proteins are unable to fold, proteasomes, not thermosomes, target these misfolded proteins for degradation, ensuring cellular homeostasis.

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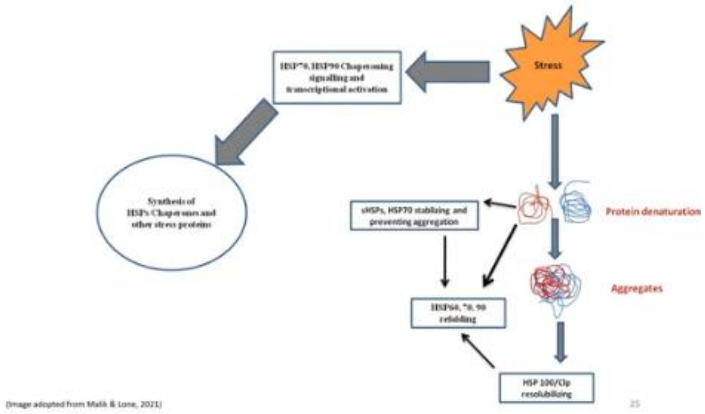
These chaperones help fold nascent or unfolded polypeptides and prevent protein aggregation. The well-studied **Hsp60** chaperonin complex (GroEL/GroES in bacteria) plays a key role in protein folding by creating a protected environment for proteins to fold properly.

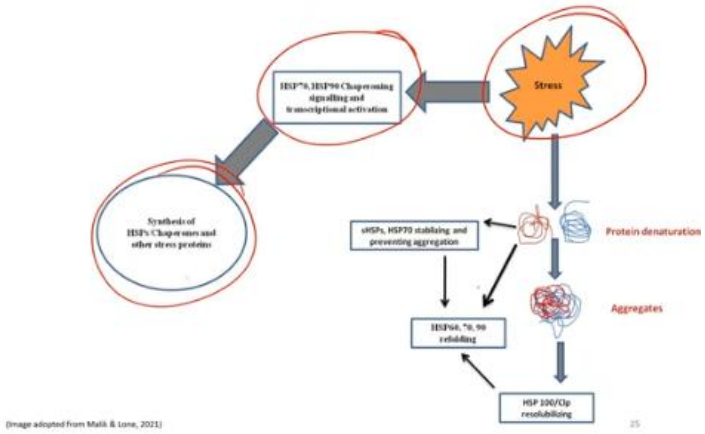
If proteins are unable to refold, **proteasomes** (not thermosomes) target these misfolded proteins for degradation, ensuring cellular homeostasis.

(Malik & Lone, 2021)

So, such proteins will be immediately gotten rid of. So, here we can see there is some stress which induces the HSP 70, 90, chaperone signaling, and then it will help in the synthesis of HSPs chaperones and other stress proteins. Then there is this HSP 70 stabilizing and preventing the aggregation. So, this protein without this will be denatured. So, this is the aggregate.



(Image adopted from Malik & Lone, 2021)



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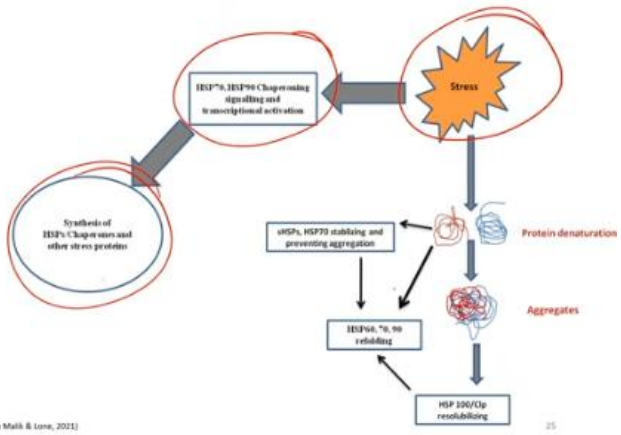

(Image adopted from Malik & Lone, 2021)

And then also 60, 70, 80, 90 will help in the refolding as discussed in the earlier slide. Thermostable proteins. Proteomic studies have revealed that protein stability in thermophiles is vital for adapting to high temperatures, especially for regulatory and catalytic proteins. Thermophiles have more disulfide bonds than mesophiles, enhancing protein stability. However, the intracellular reducing environment complicates disulfide bond formation. Genomic data suggests thermophiles possess disulfide oxidoreductase proteins which aid in stabilizing proteins through disulfide bond formation. Thermophilic enzymes possess unique architectural properties which contribute to their thermophilicity.

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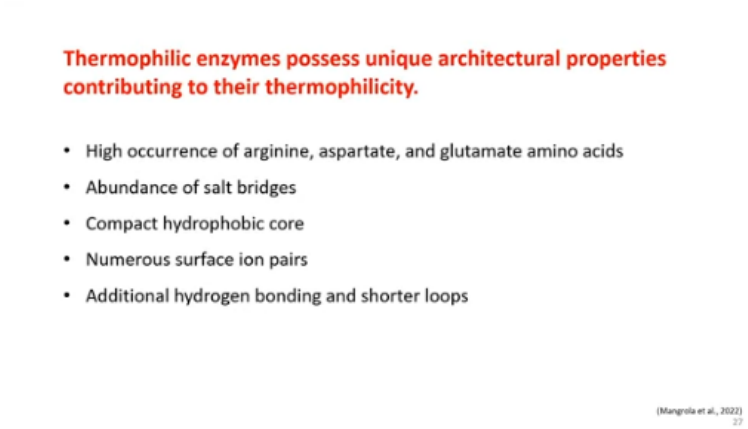
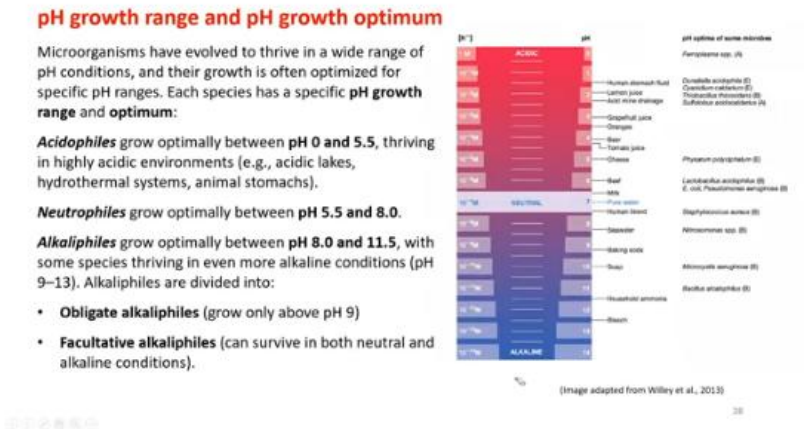
(Mangrola et al., 2022)



There is a high occurrence of arginine, aspartate, and glutamate amino acids, an abundance of salt bridges, a compact hydrophobic core, numerous surface ion pairs, additional hydrogen bonding, and shorter loops. Let us now discuss the survival of microorganisms under extreme pH conditions, what is a favorable pH growth range, and what is the optimum pH favored by certain organisms. So, if you look into this figure, as we go from the acidic to the alkaline through the neutral range at 7, here we see the pH range of certain body fluids or biological fluids. So, the pH of the human stomach fluid is somewhere here between 1 and 2. Lemon juice will be somewhere around 2.



Grapefruit will be 3. Oranges and beer will be something here. Tomato juice, seeds, and then some meat products. Milk will be somewhere near neutral. And pure water, of course, is the most neutral thing.

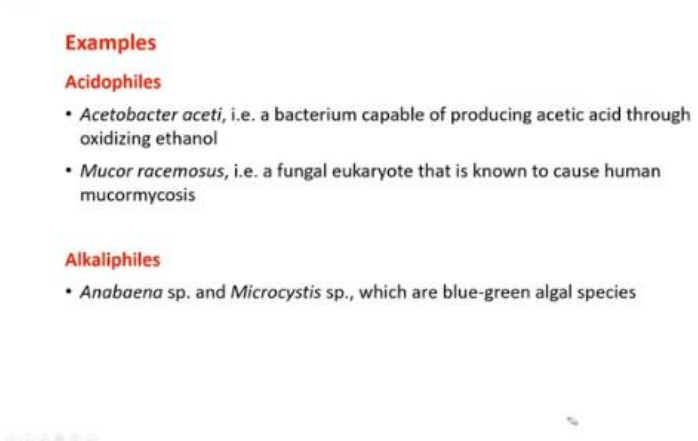
That's the standard from where we measure pH, and then human blood is slightly towards alkaline, seawater, baking soda, soap, household ammonia, bleach. So this is the scale from 1 to 14, and this is the material list which gives an idea about pH, which material has how

much of a pH. And then here is the pH optima of some of the microbes corresponding to these. So you have Ferroplasma species which survive at very low temperatures between 0 and 1. Then you have Bacillus alkaliphilus which survives around 11, then you have various others like Nitrosomonas alkaline, and then you have Lactobacillus acidophilus in slightly acidic conditions.

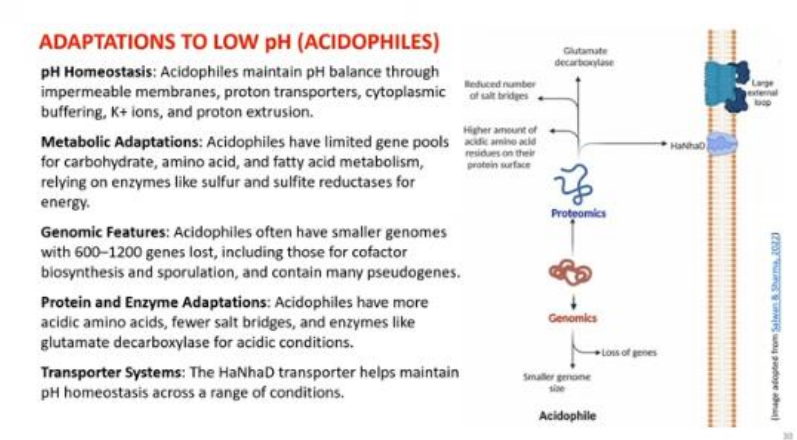
So, this gives us an idea that microbes can survive from almost 0 pH to something around 11 to 12 pH, and there is a whole list of microbes over here, and some examples are given over here. So, how do they survive in such extreme pH conditions of acidity and alkalinity? So, microbes have evolved to thrive in a wide range of these pH conditions, and their growth is often optimized for specific pH ranges. Each species has a specific pH growth range and optimum. So, those who survive in the acidic range are called acidophiles.

They grow optimally between pH 0 and 5.5. They thrive in highly acidic environments like acidic lakes, hydrothermal systems, and animal stomachs. Then there are the neutrophiles, which grow between roughly 5.5 to 8. Then there are alkaliphiles, which grow optimally between 8 to 11.5, with some species thriving in even more alkaline conditions, such as pH 9, 11, and 13. Alkaliphiles are divided into two categories.

Obligate alkaliphiles grow only above pH 9. Then there are facultative alkaliphiles, which can survive in both neutral and alkaline conditions. So we have already given examples of the acidophiles and alkaliphiles in the earlier figure. As the name suggests, Acetobacter aceti are alkaliphiles, and then you have Mucor racemosus, which are acidophiles. Additionally, you have alkaliphiles like the Anabaena species and Microcystis species, which are basically blue-green algae species. How do these microbes adapt to low pH, or how do acidophiles survive in low pH? They do it through various mechanisms or due to various features they possess.

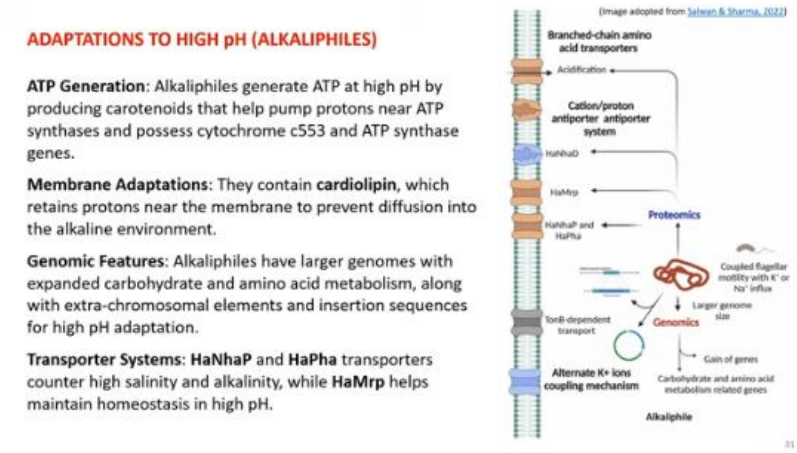


For example, they maintain pH homeostasis through impermeable membranes, proton transporters, cytoplasmic buffering, potassium ions, and proton extrusion. They also adapt their metabolic activities, or metabolic adaptations are present. They have limited gene pools for carbohydrate, amino acid, and fatty acid metabolism. They rely on enzymes like sulfur and sulfite reductase for energy production processes. And then their genomic features are something unique.

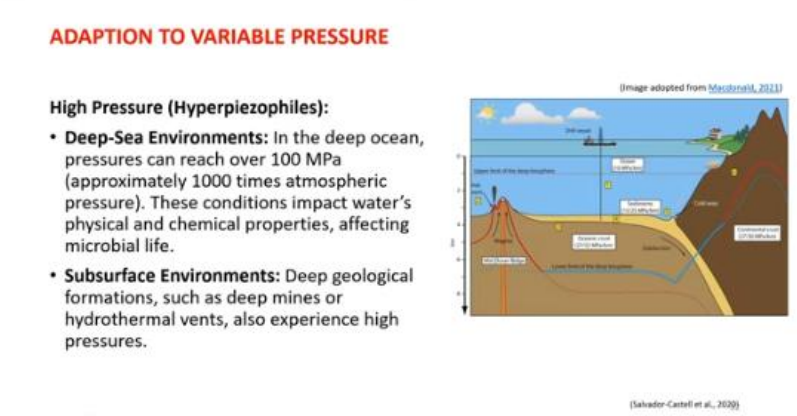


They have smaller genomes, 600 to 1200 genes lost, including those for cofactor biosynthesis and sporulation, and contain many pseudogenes. This kind of evolution may be backward evolution or devolution. Then, protein and enzyme adaptations: acidophiles have more acidic amino acids, fewer salt bridges, and enzymes like glutamate decarboxylase for acidic conditions. Then, they have transporter systems. The HaNhaD transporter helps maintain pH homeostasis across a range of conditions.

So, these are the various adaptations and strategies adopted by acidophiles. Then also, their counterparts, the alkaliphiles, have similar or some specific adaptation mechanisms. For example, the alkaliphiles generate ATP at high pH by producing carotenoids that help pump protons near ATP synthases and possess cytochrome c553 and ATP synthase genes. Then, they have their membrane adaptations, which contain cardiolipin that retains protons near the membrane to prevent diffusion into the alkaline environment. Then, there are certain genomic features.



Alkaliphiles have larger genomes compared to acidophiles, with expanded carbohydrate and amino acid metabolism, along with extrachromosomal elements and insertion sequences for high pH adaptation. And, as in the last case, they have transporter systems: HaNhaP and HaPha transporters. They counter high salinity and alkalinity, and there is a HaMrp which helps maintain homeostasis in high pH. So, these are the various transporter systems, as you can see, which help maintain homeostasis in alkaline pH. Let us now discuss the adaptation of microbes to high pressure or variable pressure.

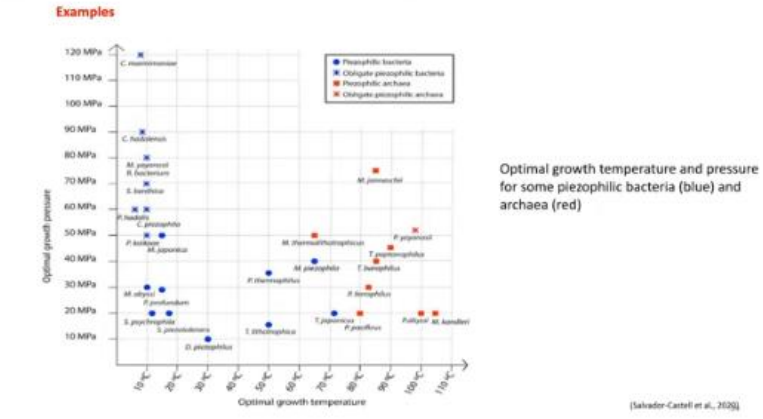


For example, they are found in deep-sea environments. These are the hyperpiezophiles. In the deep sea, pressure can reach over 100 megapascals, approximately 1000 times the atmospheric pressure. These conditions impact water's physical and chemical properties, affecting microbial life. So in these subsurface environments, deep geological formations such as deep mines or hydrothermal vents also experience high pressure.

And then there are low-pressure areas where these organisms survive. These are known as hypopiezophiles. For example, in high-altitude environments in the mountains like Everest,

atmospheric pressure drops significantly. At the summit of Mount Everest, which is around 8,900 meters above sea level, the atmospheric pressure is only about one-third of that at sea level. And then in space and high-altitude atmospheres, the vacuum of space and the near-vacuum conditions in high-altitude environments present extreme low-pressure conditions that can challenge microbial survival.

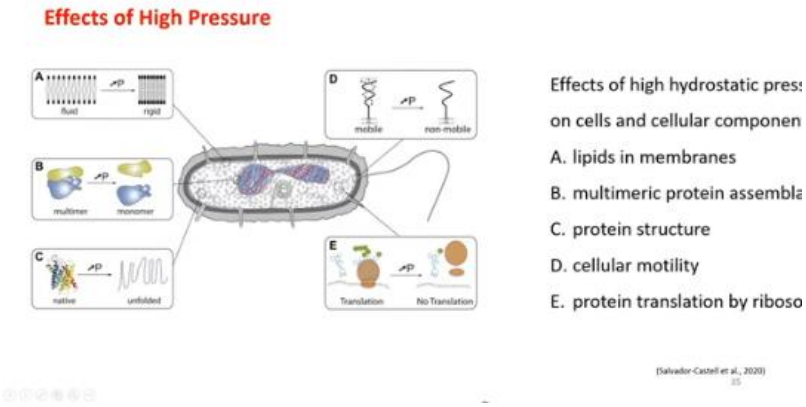
So this is a graph of optimal growth temperature and pressure for some piezophilic bacteria, blue. And then Archaea, which are red. And as you can see, their preferences are very distinct. So they can survive at, say, 10 degrees centigrade and up to 120 megapascals. And here, these are surviving around 110 degrees centigrade under something like 20 megapascals.



Optimal growth temperature and pressure for some piezophilic bacteria (blue) and archaea (red)

[Salvador-Castell et al., 2020]

So, what are the effects of high pressure on the cellular components? So, high hydrostatic pressure affects several components inside the cell. For example, under high pressure, the lipids in the membranes will be affected. The lipids are fluidic, as we know, in the membrane, but due to increased pressure, they may become compacted and rigid. So, high pressure increases rigidity, reduces fluidity, and affects the membrane protein function.



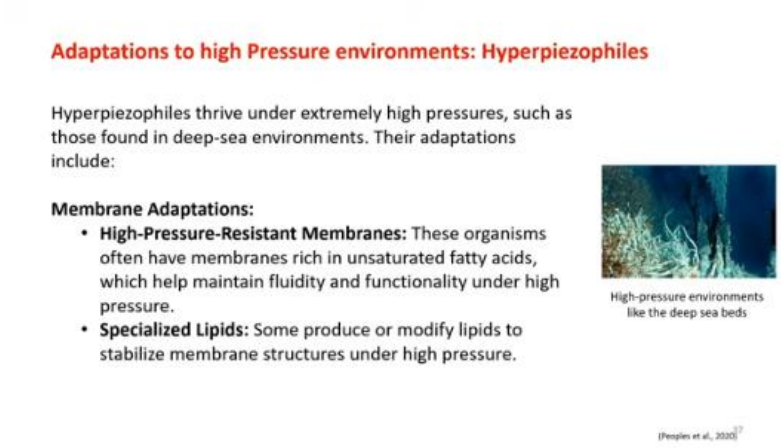
Then, in the case of multimeric proteins, high pressure may disrupt protein subunit assembly and protein-protein interactions. So, they will be disrupted, and they won't come together, making them non-functional. Then, protein structure can also be affected. This is a native protein. Due to higher pressure, the protein becomes unfolded.

So, it can denature proteins, causing misfolding and aggregation, and then the cellular motility is affected. Pressure impairs the flagella function. The flagella won't be able to function properly, and even within the cell, the cytoskeleton dynamics and ATPase activity will all be affected, resulting in the movement and also the cell division. So, due to a mobile component, due to high pressure, it will become non-mobile. Then, finally, high pressure affects protein translation.

This is very interesting. It slows translation. So, this is high pressure. So, this is normal translation happening due to high pressure. There will be no translation.

So, how does it happen? It destabilizes ribosomes and translation factors, reducing protein synthesis efficiency, probably as these multimeric proteins are not allowed to come together or they are disrupted. Similarly, the ribosome machinery will also be affected, thereby stopping protein translation. So, we can see the Effect of pressure on the cellular components is very diverse, as it actually restricts growth or almost makes life impossible for microbes.

So, how do these microbes adapt to such high-pressure or low-pressure environments? So, let us discuss the hyperpiezophiles. First, they thrive under extremely high-pressure conditions. Such as those found in deep-sea environments. And some of the adaptation mechanisms include membrane adaptations.



So, as the membrane is disrupted, we have discussed. So, high-pressure-resistant membranes have evolved. These organisms often have membranes rich in saturated fatty acids, which help maintain fluidity and functionality under high pressure. Then, there are specialized lipids. Some produce or modify lipids to stabilize membrane structures under high pressure.

Then, there are protein adaptations. As we have seen, the proteins are either unfolded or there is disruption in the multimers. So, here pressure-stable proteins are being evolved or adapted, and they are stable and functional under high pressure, often through more compact structures. Then, there is the evolution of chaperone proteins; they produce chaperone proteins that assist in maintaining proper protein folding. Adaptations to low-pressure environments, hypopiezophiles.

So, this is a new area of research with implications for predicting microbial activity in cloud and bulk atmosphere on Earth and for modeling the forward contamination of planetary surfaces like Mars. So, here also, there are pressure-responsive stress proteins. These organisms produce general stress proteins, not specifically for high pressure. Membrane adaptations like reduced membrane fluidity; they may not have specialized adaptations to increased membrane fluidity under high pressure. Low-pressure enzyme efficiency; enzymes in these organisms are optimized for normal pressure and may not perform well under high pressure.

ADAPTATIONS TO LOW PRESSURE ENVIRONMENTS: HYPOPIEZOPHILE

Bacterial growth at low pressure is a new research area with implications for predicting microbial activity in clouds and the bulk atmosphere on Earth and for modeling the forward contamination of planetary surfaces like Mars.

(Schwendner & Schuerger, 2020)

ADAPTATIONS TO LOW PRESSURE ENVIRONMENTS: HYPOPIEZOPHILE

- **Pressure-Responsive Stress Proteins:** These organisms produce general stress proteins, though not specifically for high pressure.
- **Membrane Adaptations like reduced Membrane Fluidity:** They may not have specialized adaptations to increase membrane fluidity under high pressure.
- **Low-Pressure Enzyme Efficiency:** Enzymes in these organisms are optimized for normal pressure and may not perform well under high pressure
- **Habitat Selection:** They avoid high-pressure environments by inhabiting areas with normal or low pressures.

(Schwendner & Schuerger, 2020)

Then there is habitat selection; they avoid high-pressure environments by inhabiting areas with normal or low pressures. So with this, we come to the end of this lecture on extremophiles. Thank you for your patient hearing.