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From Hot Springs to Polar Seas: The Adaptive Potential of Aquatic Biofilms in Extreme Habitats

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Abstract

Aquatic biofilms are complex microbial communities that thrive in diverse ecosystems, including some of the most extreme habitats on Earth. From geothermal hot springs and hypersaline lakes to polar seas and deep-sea hydrothermal vents, extremophilic biofilms demonstrate remarkable structural and functional resilience. Their adaptive potential is mediated by unique physiological strategies such as extracellular polymeric substance (EPS) production, stress-responsive gene regulation, and metabolic flexibility. These adaptations not only ensure survival under conditions of high temperature, salinity, pressure, or cold, but also drive ecosystem functions such as nutrient cycling and primary production. Furthermore, extremophilic biofilms hold promising applications in bioremediation, industrial biotechnology, astrobiology, and medical innovation. This article explores the adaptive mechanisms of aquatic biofilms in extreme environments, highlighting their ecological significance and biotechnological potential. Understanding these resilient microbial communities enhances our knowledge of life's boundaries on Earth and informs the search for extraterrestrial life in analogous extreme habitats.

1. Introduction

Aquatic biofilms are complex microbial assemblages embedded within a self-produced extracellular polymeric matrix that adhere to submerged surfaces. They are ubiquitous in aquatic ecosystems, playing vital roles in nutrient cycling, biogeochemical transformations, and ecosystem stability (Flemming et al., 2016). While traditionally studied in temperate environments, biofilms also thrive in extreme aquatic habitats characterized by high or low temperature, high salinity, high hydrostatic pressure, or extreme pH. These conditions, once considered too harsh to sustain microbial life, are now recognized as hotspots of microbial diversity and resilience (Merino et al., 2019). The study of biofilms in extreme environments is significant for multiple reasons. First, their adaptive potential sheds light on microbial survival strategies under stress conditions. Mechanisms such as extracellular polymeric substance (EPS) production, horizontal gene transfer, and metabolic plasticity enable

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biofilms to withstand thermal fluctuations, osmotic stress, and toxic chemical exposure (Atmakuri et al., 2024). Second, biofilms from extreme habitats play essential ecological roles, such as mediating sulfur and nitrogen cycling in hydrothermal vents or sustaining productivity in polar aquatic ecosystems. Beyond ecology, these resilient biofilms have implications in biotechnology and astrobiology. Extremophilic biofilm communities produce enzymes and metabolites (termed extremozymes) with potential applications in pharmaceuticals, bioenergy, and industrial catalysis (Elleuche et al., 2014). Moreover, their ability to thrive in environments analogous to extraterrestrial conditions has made them key models in the search for life beyond Earth (Merino et al., 2019).

2. Characteristics of Extreme Aquatic Environments

Aquatic environments considered “extreme” are defined by physical or chemical conditions that exceed the

tolerance limits of most organisms. However, biofilms through structural, physiological, and ecological adaptations (Table 1) are able to colonize such habitats and even thrive under these stresses (Merino et al., 2019). Extreme aquatic ecosystems vary widely, and the conditions encountered can act singly or in combination, generating unique selective pressures.

2.1. High-temperature environments

Hydrothermal vents, hot springs, and geothermal pools often exceed temperatures of 80–120°C. Biofilms in these habitats are dominated by thermophilic bacteria and archaea, such as *Aquificales* and *Thermoprotei*, which exploit chemolithoautotrophic pathways. Extracellular polymeric substances (EPS) protect cells from thermal fluctuations, while thermostable enzymes enable efficient metabolism.

2.2. Low-temperature environments

Polar oceans, alpine lakes, and deep cryo-environments

Table 1: Adaptations of various microbes (extremophiles) to colonize extreme habitats

Environment	Major stressor(s)	Microorganisms	Notable adaptations
Hydrothermal vents	High temperature, pressure	<i>Thermococcus</i> , <i>Pyrococcus</i>	Heat-stable enzymes, specialized membranes
Polar seas/sea ice	Sub-zero temperatures, salinity	<i>Colwellia psychrerythraea</i>	Antifreeze proteins, EPS protection
Soda lakes	High alkalinity (pH > 10)	<i>Spirulina</i> , <i>Halomonas</i>	pH homeostasis, ion transporters
Acidic hot springs	Low pH, heavy metals	<i>Acidithiobacillus</i> , <i>Sulfolobus</i>	Acid-stable enzymes, metal resistance
Deep-sea sediments	High pressure, nutrient scarcity	<i>Shewanella</i> , <i>Desulfovibrio</i>	Pressure-tolerant proteins, slow metabolism

remain below 5 °C year-round. Here, psychrophilic biofilms form on submerged rocks, sea ice, and sediments. Their EPS contain cryoprotectants, antifreeze proteins, and unsaturated fatty acids that maintain membrane fluidity. Biofilms in polar seas also serve as primary producers, hosting photosynthetic diatoms and cyanobacteria that sustain food webs.

2.3. High-salinity environments

Deep-sea trenches and abyssal plains subject biofilms to hydrostatic pressures exceeding 100 MPa. Piezophilic (barophilic) biofilms exhibit structural adaptations in membrane proteins and ribosomes, maintaining stability under compression. Biofilms colonizing seafloor rocks and sediments often participate in methane and sulfur cycling, critical for deep-sea ecosystems.

2.4. Extreme pH environments

Acidic environments, such as acid mine drainage systems (pH < 3) and alkaline soda lakes (pH > 10), harbour biofilms with remarkable tolerance. Acidophilic biofilms resist metal toxicity through EPS-mediated metal sequestration and efflux pumps. Conversely, alkaliphilic biofilms use specialized ion pumps and buffering EPS to maintain pH homeostasis (Sorokin et al., 2014).

2.5. Multiple stressors and polyextremophily

Biofilms display remarkable resilience in extreme aquatic environments, owing to a combination of structural, physiological, genetic, and community-level strategies. These mechanisms enable microbial consortia to tolerate high stress levels that would be lethal to planktonic cells, ensuring long-term survival and ecological stability (Flemming et al., 2016).

3. Mechanisms of Biofilm Resilience

Biofilms display remarkable resilience in extreme aquatic environments, owing to a combination of structural, physiological, genetic, and community-level strategies. These mechanisms (Figure 1) enable microbial consortia to tolerate high stress levels that would be lethal to planktonic cells, ensuring long-term survival and ecological stability (Flemming et al., 2016).

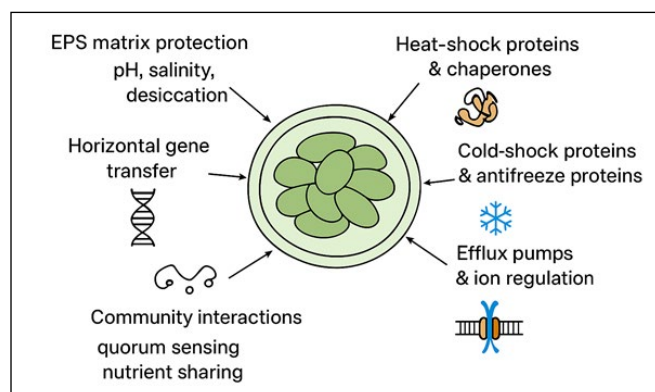


Figure 1: Resilience mechanisms in extreme aquatic biofilms

3.1. Structural adaptations: the role of EPS matrix

The extracellular polymeric substances (EPS) matrix is a defining feature of biofilms and a key factor in their resilience. EPS, composed of polysaccharides, proteins, nucleic acids, and lipids, acts as a protective barrier against thermal fluctuations, desiccation, pH stress, and toxic metals. In high-salinity environments, EPS facilitates osmotic balance by trapping water molecules, while in acidic or metal-rich habitats, EPS binds toxic ions, reducing their bioavailability (Atmakuri et al., 2024). The matrix also stabilizes biofilm architecture, providing mechanical strength under high-pressure conditions such as deep-sea trenches.

3.2. Physiological and biochemical mechanisms

Extreme aquatic biofilms employ diverse physiological strategies to withstand stress. Psychrophilic biofilms produce antifreeze proteins, exopolysaccharides, and unsaturated fatty acids to maintain membrane fluidity at low temperatures. Thermophilic biofilms rely on heat-shock proteins, chaperones, and thermostable enzymes that preserve protein structure at $>80^{\circ}\text{C}$. Halophilic biofilms accumulate compatible solutes such as glycine betaine, trehalose, and ectoine to counteract osmotic stress. Acidophilic and alkaliphilic biofilms use proton/

sodium pumps and cytoplasmic buffering compounds to maintain internal pH stability (Sorokin et al., 2014).

3.3. Genetic and molecular mechanisms

At the genetic level, resilience is supported by high genomic plasticity and adaptive regulatory pathways. Horizontal gene transfer (HGT) within biofilms accelerates the acquisition of stress-resistance genes. Quorum sensing coordinates collective responses, regulating EPS production, stress proteins, and secondary metabolites. Stress response regulons, such as heat-shock proteins (*hsp*), cold-shock proteins (*csp*), and oxidative stress pathways, allow rapid adaptation to fluctuating conditions. Biofilm-associated archaea in hydrothermal vents exhibit unique metabolic pathways for sulfur and methane utilization, enhancing survival under nutrient-limited extremes.

3.4. Community-level resilience

Resilience is not only a property of individual microbes but also of the biofilm community as a whole. Functional redundancy ensures that if one species is inhibited by stress, others can compensate, maintaining ecosystem function. Mutualistic interactions between bacteria, archaea, and eukaryotes provide metabolic complementation, such as hydrogen transfer or nutrient sharing. Spatial heterogeneity within biofilms creates microenvironments (e.g., oxygen or pH gradients), allowing diverse species to coexist under extreme conditions. Dormancy and persister cell formation allow subsets of the community to survive until favorable conditions return.

3.5. Evolutionary adaptation

Over evolutionary timescales, biofilms in extreme aquatic habitats exhibit signatures of selection for stress resistance. Genomic studies of extremophiles have revealed unique gene clusters encoding extremozymes, transport systems, and resistance factors that are often absent in mesophilic microbes (Cavicchioli et al., 2019). Such adaptations not only enhance survival but also expand the ecological niches biofilms can colonize.

4. Ecological and Biogeochemical Roles of Extreme Biofilms

Aquatic biofilms in extreme environments are not only resilient survivors but also vital contributors to ecosystem functioning. By mediating nutrient cycles, supporting productivity, and shaping habitat structures, these microbial assemblages serve as keystone players in environments where higher life forms are scarce or absent.

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Their metabolic versatility and community interactions enable the maintenance of ecological balance in otherwise hostile habitats.

4.1. Primary production and energy flow

In extreme aquatic ecosystems where planktonic communities are limited, biofilms often serve as primary producers. In polar seas and alpine lakes, phototrophic diatoms and cyanobacteria embedded within biofilms perform photosynthesis under low light and subzero conditions, sustaining local food webs. Chemolithoautotrophic biofilms in hydrothermal vents and acidic mine waters, biofilms dominated by archaea and bacteria (e.g., *Sulfolobus*, *Thiobacillus*) fix CO₂ by oxidizing sulfur, iron, or methane, providing energy for entire ecosystems.

4.2. Nutrient cycling

Psychrophilic biofilms in polar regions sequester carbon in EPS, acting as carbon sinks, while deep-sea biofilms regulate methane flux through anaerobic methane oxidation (Orcutt et al., 2011). Nitrifying and denitrifying biofilms in hot springs and soda lakes mediate nitrogen transformations under extreme temperatures and alkalinity. Hydrothermal vent biofilms oxidize reduced sulfur compounds (H₂S), fueling chemosynthetic communities and influencing ocean sulfur dynamics.

4.3. Habitat engineering

Biofilms act as ecosystem engineers by modifying physical and chemical conditions. EPS layers trap sediments, forming microbial mats in hot springs and hypersaline lakes that stabilize substrates and create microhabitats. Biofilms generate microgradients of oxygen, pH, and nutrients, enabling the coexistence of metabolically diverse species within a single matrix (Flemming et al., 2016). In deep-sea vents, biofilm-associated structures serve as habitats for invertebrates, including tubeworms, clams, and shrimp, which underpin complex food webs.

4.4. Ecosystem resilience and stability

Biofilms enhance ecosystem resilience by buffering extreme fluctuations. In polar ecosystems, the seasonal melting of ice releases biofilm-derived nutrients that sustain phytoplankton blooms (Boetius et al., 2015). In hypersaline or acidic systems, biofilms maintain metabolic activity even under severe stress, supporting microbial diversity and preventing ecological collapse. Biofilms' functional redundancy ensures continuity of ecosystem services (e.g., nitrogen fixation, carbon sequestration)

even when individual taxa are lost.

4.5. Global and planetary implications

The ecological roles of extreme biofilms extend beyond local ecosystems to broader Earth systems and planetary science. Deep-sea biofilms influence climate-relevant processes, including methane cycling and carbon storage (Orcutt et al., 2011). Ancient stromatolitic biofilms in hypersaline lakes provide analogues for early Earth microbial ecosystems. Their resilience in polyextreme conditions makes them strong candidates in the search for extraterrestrial life on Mars, Europa, and Enceladus (Merino et al., 2019).

5. Biotechnological and Applied Implications

Extreme aquatic biofilms are reservoirs of novel biomolecules, enzymes, and adaptive strategies that have broad applications in biotechnology, industry, and planetary exploration. Their unique resilience to multiple stressors has made them attractive models for bioremediation, enzyme discovery, pharmaceuticals, and astrobiology (Elleuche et al., 2014).

5.1. Extremozymes and industrial applications

Biofilms inhabiting extreme environments produce enzymes commonly referred to as extremozymes with remarkable stability under harsh conditions that denature conventional enzymes. Thermozymes from thermophilic biofilms in hot springs are used in polymerase chain reaction (PCR), detergent formulations, and food processing. Psychrozymes from polar biofilms retain catalytic activity at subzero temperatures, useful in cold-wash detergents, food preservation, and biotransformations requiring low-temperature stability (Cavicchioli et al., 2019). Halophilic enzymes from hypersaline biofilms have industrial applications in bioplastics, tanning, and biofuels due to their salt tolerance. Alkaliphilic and acidophilic enzymes are applied in textile processing, leather industries, and bioleaching of metals.

5.2. Bioremediation and environmental applications

Biofilms from extreme environments have evolved mechanisms to detoxify or immobilize pollutants, making them promising agents in bioremediation. Acidophilic biofilms from acid mine drainage sequester heavy metals such as arsenic, cadmium, and lead via EPS binding. Thermophilic and halophilic biofilms can degrade hydrocarbons and petrochemicals in oil-contaminated

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sites under high temperature or salinity. Deep-sea biofilms participate in methane oxidation and sulfate reduction, reducing greenhouse gas fluxes from marine sediments (Orcutt et al., 2011).

5.3. *Pharmaceutical and biomedical potential*

Extreme biofilms harbor microbes producing secondary metabolites with antimicrobial, anticancer, and antiviral properties. Halophilic biofilms produce carotenoids and polyhydroxyalkanoates with antioxidant and nutraceutical potential. Thermophilic biofilms generate thermostable antibiotics and novel bioactive peptides. EPS from extremophilic biofilms exhibit unique rheological properties with applications in wound healing and drug delivery.

5.4. *Biofilm-inspired materials and nanotechnology*

Biofilms in extreme habitats inspire the design of bioinspired materials. EPS properties such as high viscosity, ionic binding capacity, and self-healing behavior are being mimicked in biopolymers, hydrogels, and nanocomposites (Arora and Paliwal, 2025). Additionally, biofilms' natural ability to form conductive or mineralized structures is being explored in bioelectronics and biomineralization technologies.

5.5. *Astrobiology and space exploration*

Extreme aquatic biofilms serve as analogues for extraterrestrial life due to their ability to withstand polyextreme conditions. Biofilms in Antarctic lakes and hypersaline brines resemble potential habitats on Mars and Europa (Merino et al., 2019). Their survival under desiccation, UV radiation, and high salinity supports their role in planetary protection studies and life-detection missions. Enzymes and metabolites from these biofilms could support in-situ resource utilization (ISRU) in space missions, including bioreactors for recycling and energy production.

5.6. *Future industrial integration*

As biotechnological tools such as synthetic biology, metagenomics, and CRISPR advance, extremophilic biofilms can be engineered for tailored applications. Potential future directions include: Biofilm-based biocatalysts for sustainable chemical production, Next-generation wastewater treatment systems using polyextremophilic biofilms and Engineered biofilms designed for carbon capture and greenhouse gas mitigation.

6. Challenges and Future Perspectives

Despite the remarkable progress in understanding the

ecology, physiology, and applications of aquatic biofilms in extreme environments, several knowledge gaps and challenges remain. Addressing these issues will be crucial for advancing both fundamental science and biotechnological exploitation.

6.1. *Methodological challenges*

Studying biofilms in extreme habitats is inherently difficult due to accessibility and technical limitations. Collecting intact biofilm samples from hot springs, polar ice, or deep-sea hydrothermal vents requires specialized equipment and often alters the in-situ structure of biofilms. The vast majority of extremophilic biofilm microorganisms remain uncultivable under laboratory conditions, limiting functional studies. Omics-based approaches generate massive datasets, but integrating metagenomics, metatranscriptomics, and metabolomics into a coherent picture of biofilm function remains challenging.

6.2. *Environmental and ecological complexity*

Extreme biofilms rarely exist in isolation but rather function as complex microbial consortia shaped by dynamic and fluctuating environmental conditions. Many extreme habitats exhibit polyextremophily, where multiple stressors such as high temperature, pressure, and salinity coexist, as in hydrothermal vents, complicating predictions of microbial resilience and adaptive limits (Merino et al., 2019). The ecological significance of community interactions, including microbial cooperation, competition, and horizontal gene transfer, is still not fully understood, yet these processes likely play a pivotal role in enhancing biofilm stability and adaptability. In addition, the accelerating impacts of climate change, including polar sea warming, permafrost melting, and ocean acidification, pose significant threats to the stability of extremophilic biofilms, with potential consequences for nutrient cycling, carbon sequestration, and broader ecosystem functioning.

6.3. *Risks and biosecurity concerns*

While extremophilic biofilms hold tremendous promise for biotechnology and environmental applications, their exploitation and use also pose potential risks. Bioprospecting ethics remain a major concern, as unsustainable harvesting from fragile habitats such as Antarctic lakes or deep-sea hydrothermal vents could lead to irreversible biodiversity loss. In industrial contexts, some extremophilic biofilms contribute to biocorrosion, accelerating the degradation of pipelines, ships, and

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submerged infrastructure, thereby generating significant economic and engineering challenges (Little and Lee, 2015). Furthermore, the application of extremophilic traits through genetic engineering or synthetic biology carries a biohazard potential, as accidental release or containment failure could result in unintended ecological consequences. Balancing innovation with responsible stewardship is therefore essential to ensure that the benefits of extremophilic biofilms are realized without compromising environmental integrity or human safety.

6.4. Future research directions

To address current challenges, future research on extremophilic aquatic biofilms must adopt interdisciplinary and integrative approaches that bridge ecology, biotechnology, and astrobiology. Advances in omics and single-cell technologies, including high-resolution sequencing, imaging, and isotope tracing, will enable unprecedented insights into the metabolic networks and functional dynamics of biofilm communities. Harnessing synthetic biology and metabolic engineering offers opportunities to design tailored biofilms with enhanced resilience, paving the way for transformative applications in wastewater treatment, bioremediation, and industrial biotechnology. Equally important are climate resilience studies, which can reveal how biofilms respond to rapid changes in temperature, salinity, and pH, thereby improving predictions of ecosystem stability under global change. Integrating astrobiology perspectives will further position aquatic biofilms as valuable analogs for extraterrestrial life, guiding exploration and life-detection strategies on Mars, Europa, and Enceladus. Finally, ensuring sustainable exploitation through ethical bioprospecting frameworks will be essential for conserving sensitive extreme ecosystems while responsibly unlocking their biotechnological potential.

7. Conclusion

Aquatic biofilms in extreme environments exemplify resilience, thriving under heat, cold, salinity, pressure, and pH through unique structural, physiological, and genetic strategies. They stabilize ecosystems, drive nutrient cycling, and promise advances in bioremediation, industrial enzyme production, and medical innovation, while serving as analogs for extraterrestrial life. As pioneers of adaptation, they highlight life's plasticity and innovation. Future discoveries, supported by advanced and sustainable approaches, will expand understanding,

enable applied breakthroughs, and ensure conservation of these remarkable microbial systems.

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