TERRESTRIAL PERMAFROST AS A MODEL FOR MICROBIAL GROWTH AT LOW TEMPERATURES: IMPLICATIONS FOR MARS EXTANT LIFE.

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Introduction: Terrestrial permafrost is a useful model for the growth and survival of microorganisms under long-term low temperature conditions. Arctic permafrost has remained frozen at 0 to -13°C at depth for up to ~3 million years [1]; while Antarctic permafrost is only found in the Dry Valleys and the Antarctic peninsula, generally experiences colder temperatures, and in some areas may be 5 to 8.1 million years old [2].

Living in Permafrost: For microorganisms, the defining character of permafrost is its frozen state, which presents organisms with the combined stresses of low temperatures and a confined matrix. As temperatures decrease molecules become less flexible and reaction rates decrease. In a frozen matrix, liquid water is limited and confined to thin briny veins and films between ice crystals and minerals which also leads to the reduced diffusion of nutrients. Conditions in permafrost can be permissive or nonpermissive for microbial metabolism as in the two case studies below.

Permissive conditions. Many microorganisms have been isolated from organic-rich Arctic permafrost [3-5], demonstrating that survival of these long-term low-temperature low-diffusion conditions is frequently realized. The isolation of undamaged DNA from 500,000 year old permafrost when DNA should be highly degraded within 100,000 years under these conditions indicates that cells must be active to survive long-term burial. Indeed, long-term burial in permafrost selects against endospores which have no active metabolism [5]. Furthermore, an increase in acetate concentration with age from 2,000 to 134,000 years in Siberian permafrost suggests ongoing microbial fermentation of carbon under anoxic conditions [6].

Nonpermissive conditions. In University Valley (UV), Antarctica, the valley floor contains both dry and ice-cemented permafrost ranging in age from 10^4-10^5 years. The presence of active microorganisms has not be demonstrated [7]; UV permafrost is likely too dry and too cold to sustain microbial life. In UV permafrost water exists primarily as interfacial water; bulk water (as thin films) is only present for about 74 hours a year when temperatures in surface soils rise to -1°C.

Implications for Mars Extant Life: If mars extant life has a similar basis to terrestrial life and martian permafrost is a potential habitat, the following characteristics are suggested by observations of terrestrial permafrost:

Some time at permissive conditions is required. Arctic permafrost has permissive temperatures and sufficient liquid water. UV permafrost is too cold and too dry, with not enough time at permissive temperature and water conditions. At permissive temperatures, microorganisms may persist for a very long time given adequate water and nutrients.

Few nutrients are required for active persistence. Carbon in organic rich Arctic permafrost is not noticeably decomposed while frozen [8, 9] (except see above), suggesting that organisms are consuming very few nutrients. (The high organic content may provide other protective effects such as steeper concentration gradients of nutrients or increased water activity.)

Adaptation to frozen conditions is "incomplete." Slow rates of metabolism combined with the relatively young age of permafrost and other frozen environments limit the ability of organisms to evolve. Instead, the inhabitants of modern permafrost likely evolved from mesophiles to survive extreme low temperature conditions and exploit more clement conditions as they arise.

Organisms tolerate broad temperature ranges. Most permafrost underlies an "active layer" which freezes and thaws seasonally and much of Arctic permafrost was once active layer. Active layer survival likely exerts a significant selective force on microorganisms and, not surprisingly, most Arctic permafrost isolates tolerate a broad range of cold temperatures.

Organisms are halotolerant rather than halophilic. Any liquid water present at temperatures below freezing likely has a high solute concentration (mostly salts) due to freezing point depression. Organisms isolated from permafrost tend to be halotolerant rather than halophilic, likely because of the range of salt concentrations experienced in the active layer (see above).

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