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Stable Carbon Isotope Fractionation During Steady-State Methanogenesis as a Function of DIC Concentration

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Autotrophic methanogenesis, or the biological conversion of carbon dioxide (CO_2) to methane, is an ancestral metabolism found in a specific group of anaerobic archaea called methanogens. Methanogens live in a wide range of chemical systems and are often found in extreme environments. One such extreme environment is a serpentinizing system, where water-rock reactions create (hyper)alkaline, hydrogen-replete, and carbon-limited conditions. Although carbon-limitation is prevalent in these astrobiologically and early Earth relevant extreme environments, most experiments investigating carbon isotope fractionation in microbes have focused on carbon-replete systems. Additionally, the majority of isotope fractionation studies use closed-system and fast growth laboratory experimental set-ups that do not represent natural conditions. Here we test the impact of carbon-limitation on the carbon isotope fractionation between CO_2 and methanogenesis products produced during steady-state through chemically static (chemostat) continuous culture experiments. We varied the amount of CO_2 available to the methanogen species *Methanococcus maripaludis* while keeping a constant slow growth rate to create conditions ranging from carbon-replete to carbon-limited. The data show that carbon isotope fractionation between methanogenesis products and aqueous CO_2 is a factor of carbon availability, with decreasing carbon availability causing greater fractionation between the two pools. Additionally, we see that the energetic state of the system is not heavily impacted by carbon-availability and that methanogenesis is a thermodynamically favorable reaction in carbon-limited conditions if there is sufficient H_2 present. We created an isotope flux model to explain the differences in carbon isotope fractionation that shows how the flux of CO_2 between the gaseous and aqueous pools, the diffusion of CO_2 in and out of the cell, and the kinetic fractionation of methanogenesis steps all impact the fractionation of methanogenesis products from source CO_2. Overall, these results show that methanogenesis has the thermodynamic potential to be favorable in extremely carbon-limited conditions and provide insights into how methanogen $d^{13}C$ biosignatures reflect the degree of carbon-availability in the environment.

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