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Importance of midday photomixotrophy by *Roseiflexus* spp. to the ^{13}C content of hot spring cyanobacterial mats

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Microbial mats inhabiting extreme environments can serve as analogs for ancient stromatolites or for better understanding microbial interactions at the fringes of the habitable zone. Here, we use mats from two hydrothermal systems at Yellowstone National Park (Octopus Spring and Mushroom Spring) to test the hypothesis that multiple microorganisms, vertically stratified within the mat's layers can utilize different light wavelengths to simultaneously perform phototrophy during daylight. The benthic mats inhabiting the outflow channels of these springs are predominated by unicellular photoautotrophic cyanobacteria (*Synechococcus* spp.), which were historically thought to cross-feed photoheterothrophic filamentous phototrophic bacteria (mainly *Roseiflexus* spp.), except under early morning anoxic conditions when *Roseiflexus* has been shown to fix dissolved inorganic carbon (DIC). However, transcription patterns challenge the pre-exiting understanding of the system by suggesting that *Roseiflexus* spp. may perform daytime photomixotrophy, in which DIC is incorporated together with organic compounds. We performed ^{13}C tracer studies over a daylight cycle to establish the timing of and roles played by *Synechococcus* spp. and *Roseiflexus* spp. in DIC and organic matter uptake in mid-day light and oxic mats. Samples were incubated under *in situ* conditions with either full (control incubations) or filtered (experimental) light intended to target distinct photoreceptors. Isotope ratio mass spectrometry (IRMS) showed that ^{13}C-bicarbonate uptake into the mat under infrared (IR) light (utilized by anoxygenic phototrophs) or visible-minus-blue light (used by cyanobacteria) was about half that incorporated in full light. Laser ablation IRMS (LA-IRMS) analysis demonstrated that ^{13}C incorporation under visible-minus-blue light was restricted to the uppermost portion of the mat, whereas ^{13}C incorporation under IR light was maximal in deeper mat layers; consistent with the respective vertical organization of *Synechococcus* spp. and *Roseiflexus* spp.. ^{13}C-acetate, -propionate, -lactate, -and glycolate were incorporated into mat biomass at equal or greater extent under IR and full light. ^{13}C tracer analysis of peptides demonstrated DIC uptake in both *Synechococcus* spp. and *Roseiflexus* spp., whereas *Roseiflexus* spp. also exhibited uptake of ^{13}C-organic acids, especially glycolate and lactate into peptides. The potential for simultaneous autotrophic pathways, with different isotopic fractionation factors, necessitates careful interpretation of preserved $\delta^{13}C$ signatures for evaluating C cycling.