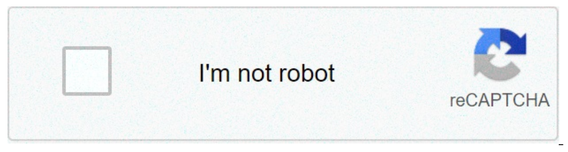

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Chemical formula for chemosynthesis

Photosynthesis and chemosynthesis are both processes by which organisms produce food; photosynthesis is powered by sunlight while chemosynthesis runs on chemical energy. To view this video please enable JavaScript, and consider upgrading to a web browser that supports HTML5 video The majority of life on the planet is based in a food chain which revolves around sunlight, as plants make food via photosynthesis. In the deep ocean, however, there is no light and thus there are no plants; so instead of sunlight being the primary form of energy, chemical energy is produced via chemosynthesis. Places with chemosynthetic organisms can become oases of life in an environment often otherwise depleted of food. Video courtesy of the NOAA Office of Ocean Exploration and Research, Gulf of Mexico 2017. Download larger version (mp4, 108.2 MB). Ecosystems depend upon the ability of some organisms to convert inorganic compounds into food that other organisms can then exploit (or eat!). The majority of life on the planet is based on a food chain which revolves around sunlight, as plants make food via photosynthesis. However, in environments where there is no sunlight and thus no plants, organisms instead rely on primary production through a process called chemosynthesis, which runs on chemical energy. Together, photosynthesis and chemosynthesis fuel all life on Earth. Photosynthesis occurs in plants and some bacteria, wherever there is sufficient sunlight – on land, in shallow water, even inside and below clear ice. All photosynthetic organisms use solar energy to turn carbon dioxide and water into sugar (food) and oxygen: 6CO2 + 6H2O -> C6H12O6 + 6O2. Chemosynthesis occurs in bacteria and other organisms and involves the use of energy released by inorganic chemical reactions to produce food. All chemosynthetic organisms use energy released by chemical reactions to make a sugar, but different species use different pathways. For example, at hydrothermal vents, vent bacteria oxidize hydrogen sulfide, add carbon dioxide and oxygen, and produce sugar, sulfur, and water: CO2 + 4H2S + O2 -> CH20 + 4S + 3H2O. Other bacteria make organic matter by reducing sulfide or oxidizing methane. Our knowledge of chemosynthetic communities is relatively new, brought to light by ocean exploration when humans first observed a vent on the deep ocean floor in 1977 and found a thriving community where there was no light. Since then, chemosynthetic bacterial communities have been found in hot springs on land and on the seafloor around hydrothermal vents, cold seeps, whale carcasses, and sunken ships. No one had ever thought to look for them, but these communities were there all along. Updated June 19, 2019 By Kevin Beck All living things require a way to produce energy in order to power the metabolic, synthetic and reproductive machinery inside their cells. Ultimately, every living thing uses the molecule ATP (adenosine triphosphate) for this purpose. In turn, to derive energy from molecules, those molecules, called nutrients, must be easy to find and simple to break down. Glucose fits this description for most life on Earth. Some organisms get glucose by digesting what they eat; others have to make it or make other carbohydrates. Far under the ocean's surface, where pressures are extreme and nutrients scarce, certain communities of organisms are able to not merely survive but thrive. Not by accident, in fact, they do so while clustering around hydrothermal vents, openings in the sea floor that emit extreme heat and chemicals that many species cannot tolerate (like miniature volcanoes). These chemosynthetic organisms represent both a curiosity and a triumph of evolution in terms of how they make food. Organisms can be classified as prokaryotes, the cells of which lack membrane-bound organelles and reproduce asexually, or eukaryotes, whose cells have their DNA enclosed in nuclei and feature a host of membrane-bound organelles in the cytoplasm. Among those membrane-bound organelles are mitochondria and, in plants, chloroplasts. Mitochondria allow all eukaryotes to break down glucose aerobically to carbon dioxide, water and energy; chloroplasts allow plants to build glucose from carbon dioxide since they cannot ingest it. Chemosynthesis is the derivation of carbon from carbon dioxide plus energy from other agents, described below. Chemosynthesis is thus closely related to photosynthesis. In fact, together, chemosynthetic organisms and photosynthetic organisms make up the autotrophs, or the class of living things that make, rather than ingest, their own food. These can be either prokaryotes or eukaryotes, as you'll see. Autotrophs are organisms that can produce, or synthesize, their own food as long as a source of carbon and a source of energy is present. This minimal source of carbon is usually in the form of carbon dioxide (CO2), a molecule that is virtually everywhere on and above the planet. Humans and other animals excrete it as waste. Plants and other autotrophs use it as fuel, maintaining one of nature's more grand and definitive biochemical cycles. Plants are the most familiar type of autotroph, but various others dot the global biosphere, often far from human eyes. Algae, phytoplankton and certain bacteria are autotrophs. In particular, the bacteria that can survive deep in the sea are of special interest because of their chemosynthetic metabolism. Chemosynthesis is a process by which energy is derived via the microbial mediation of certain chemical reactions. The source of energy for chemosynthesis is energy liberated from a chemical reaction (the oxidation of an inorganic substance) rather than energy harvested from sunlight or other light. The carbon source remains CO2, and oxygen (as O2) must be present to operate on the inorganic molecule, but that inorganic molecule may be hydrogen gas (H2), hydrogen sulfide (H2S) or ammonia (NH3), depending on the environment in question. Whatever carbohydrate is formed for the cell's use will have the form (CH2O)N, as this is true of all carbohydrates by definition. One chemosynthesis equation depicts the conversion of carbon dioxide to carbohydrate as hydrogen sulfide is oxidized to water and sulfur: CO2+ O2 + 4 H2S → CH2O + 4 S + 3 H2O Some organisms can survive in the vicinity of sea floor vents, because these emit water with a temperature of around 5 to 100 °C (41 to 212 °F). This is not precisely warm and welcoming, but inconsistent and sometimes violent heat is better than no heat at all if you have the right enzymatic equipment. Some "bacteria" in these so-called hydrothermal vent communities are actually Archaea, prokaryotic organisms closely related to bacteria (and formerly called archaebacteria). One example is Methanopyrus kandleri, which tolerates very salty and very warm environments with unusual ease. This species gets energy from hydrogen gas and releases methane (CH4). Definition noun, plural: chemosyntheses The production of a more complex chemical compound by combining two or more simpler chemical entities or precursors Supplement Biosynthesis refers to the production of a complex chemical compound from simpler precursors in a living organism. It usually involves an enzyme that will catalyze the reaction). It may also need an energy source (e.g. ATP). Examples of biosynthesis include photosynthesis, chemosynthesis, amino acid synthesis, nucleic acid synthesis, and ATP synthesis. Chemosynthesis is a biosynthesis performed by living organisms. It is through this process that a more complex chemical compound is produced. It often does so by combining simpler chemical entities or precursors. Examples of chemical synthesis, in particular, include organic synthesis and dehydration synthesis. Chemoautotrophs, for instance, are organisms that perform chemosynthesis. They include certain groups of bacteria such as sulfur-oxidizing gamma proteobacteria, epsilon proteobacteria, and neutrophilic iron-oxidizing bacteria, and certain archaea such as methanogenic archaea. Certain eukaryotes form symbiosis with bacteria that can fix carbon dioxide for them. For instance, the giant tube worms have bacteria in their trophosome that can produce sugars and amino acids from carbon dioxide with hydrogen sulfide as the energy source. This form of chemosynthesis results in the formation of carbohydrate as well as solid globules of sulfur. Also called: See also: anabolism synthesis This tutorial introduces flowing water communities, which bring new and dithering factors into the equation for possible.. The blood sugar level is regulated by two hormones. The mechanism behind this type of negative feedback control is descr.. This tutorial describes the independent assortment of chromosomes and crossing over as important events in meiosis. Read.. Lymphocytes are a type of white blood cell capable of producing a specific immune response to unique antigens. In thi.. This tutorial looks at the mutation at the gene level and the harm it may bring. Learn about single nucleotide polymorph.. Mātauranga Māori is the living knowledge system of the indigenous people of New Zealand, including the relationships t.. In-depth geophysical and geochemical exploration and lake floor mapping of Yellowstone Lake, the largest Alpine Lake in the United States, has revealed numerous sublacustrine hot vents and hydrothermal features in geothermally active areas on the lake bottom (Klump et al., 1988, 1995; Remsen et al., 1990; Morgan et al., 2003a, b). Direct observations by SCUBA and ROV have revealed a wide range of hydrothermal features, including large hydrothermal chimneys; gas fumaroles; seepage of hot, shimmering water; and sulfur-oxidizing microbial mats growing around hot water seeps and vents (Remsen et al., 2002). Examination of an ancient vent chimney revealed internal conduit structures with metal sulfide precipitates, indicating long-term hydrothermal activity (Cuhel et al., 2004). In contrast to the well-studied photosynthetic and chemosynthetic aerial hot spring communities of Yellowstone Park terrestrial habitats (Ward et al., 1998; Spear et al., 2005), systematic analyses of these Yellowstone Lake hydrothermal microbial communities are in their early stages, but have already demonstrated the potential for autotrophic, thermophilic chemosynthetic microbial communities. For example, the vents at Steamboat Point and Mary Bay at the northern edge of the lake, and deep-water vents off Stevenson island in the center of the lake, harbor chemosynthetic bacteria that assimilate dissolved inorganic carbon (DIC) in the dark at rates typically 0.08–0.5 μM C h−1, with maxima at approximately 0.75 μM C h−1 (Cuhel et al., 2002). Thus, chemosynthetic rates often exceed the photosynthetic rate at the lake surface, approximately 0.25 μM C h−1 (Cuhel et al., 2002). Microbial biodiversity in Yellowstone Lake thermal springs is largely unexplored. The isolation of the thermophilic sulfate-reducing bacterium Thermodesulfovibrio yellowstonii, a deeply branching bacterial lineage from Yellowstone Lake thermal vents, implies untapped potential for further discoveries (Henry et al., 1994). Here, we present results of a preliminary 16S rRNA gene clone library survey of the bacterial communities in five different thermal vent locations in Yellowstone Lake with distinct chemical signatures and distinct temperature-dependent chemosynthetic rates. The 16S rRNA gene clone libraries indicate the existence of distinct chemosynthetic bacterial communities, dominated either by Gammaproteobacteria affiliated with the mesophilic sulfur-oxidizing genus Thiovirga, or by phylotypes most closely related to cultured species and strains of the extremely thermophilic Aquificales. Materials and Methods Sampling and DNA Extraction Hydrothermal vent waters were collected in July 2003 from five locations (Table 1) in Yellowstone Lake for microbial community analysis by 16S rRNA gene sequencing (Table 1). The first two samples come from the Mary Bay area near the northeastern shore of the lake, one of the hydrothermally most active areas of Yellowstone Lake, with high heat flux and numerous hydrothermal vents (Morgan et al., 2003b): Mary Bay West 12 is a surface water sample taken above a nearshore bubbling warm fumarole in shallow water (1 m), and Mary Bay Canyon 28 represents warm deep water (52 m) below the sill of an underwater canyon in Mary Bay. The third and hottest water sample, Stevenson Island 72, comes from a deep trench east of Stevenson Island in the central portion of the lake, where small, well-developed hydrothermal vents coalesce along northwest-trending deep fissures that reach maximally 133 m depth, the deepest point in the lake (Morgan et al., 2003b). The fourth sample, West Thumb Canyon 129, represents hot vent water from a sublacustrine explosion crater in the western part of West Thumb basin, in the westernmost part of the lake (Morgan et al., 2003b). The fifth sample from the West Thumb Basin, West Thumb 98, represents a cooler, low activity water sample from the West Thumb area. In situ temperatures measured by ROV, and chemistry of the syringe-sampled waters are shown in Table 1. Table 1. Yellowstone Lake vent samples: summary of chemistry, dark C fixation, and 16S rRNA gene sequence data. Water was collected into 2-L polycarbonate piston-style syringe samplers mounted on a tethered ROV (Eastern Oceanics, Inc.) using an articulated arm outfitted with a thermistor probe at the end to measure the temperature of the water as it was collected (Aguilar et al., 2002). Using a checkvalve system, each piston sample was rinsed with 300–500 mL of vent sample prior to filling. The ROV is fully operator-controlled with thrusters that allow for lake floor reconnaissance and positioning for sampling, and included live video for vent identification and guided sampling (Lovalvo et al., 2010); it is deployed from RV Cutthroat, the Yellowstone Lake research vessel owned and operated by the National Park Service. Vent water samples were retrieved from the ROV collection syringes and put into smaller, all-plastic syringes through a three-way valve without exposure to air. Subsamples of 150–310 mL volume (Table 1) were used for filtration and cell capture on 0.22 μm polycarbonate filters. The filters were frozen at −80°C until DNA isolation in the laboratory in Chapel Hill, by phenol/chloroform extraction (Teske et al., 1996). Near-complete 16S rRNA genes were PCR-amplified with bacterial primers 8F (5′-AGRGTTTGATCCTGGCTCAG-3′) and 1492R (5′-CGGCTACCTTGTTACGACTT-3′); these primers were successful in recovering extremely diverse bacterial communities, including members of novel phyla (Teske et al., 2002). PCR products were cloned using the TOPO XL PCR cloning kit (Invitrogen Corporation, Carlsbad, CA, USA) following the manufacturers instructions, and sequenced at the sequencing center of the University of North Carolina with primers M13F (5′-GTAAAACGACGGCCAG-3′) and M13R (5′-CAGGAAACAGCTATGAC-3′). Chemical Analysis and Dark C Fixation Rate Measurements Analytical equipment was transported to Yellowstone National Park and set up as a field laboratory at the National Park Service Lake Station. Freshly collected samples for stable analytes were filtered through 0.2-μm filters (Supor-200, Pall Corp.) and aliquoted for the different analyses. Dissolved compounds were measured by flow injection analysis (silicate, nitrate, nitrite), ion chromatography (chloride, sulfate), and spectrophotometry (ammonium, phosphate) according to standard methods (APHA, 1992). All labile species were analyzed on site within 1 day of collection and analytical preparation. Rubber-free all polypropylene (PP) syringes with three-way valves were used to collect water from the 2-L ROV-mounted piston syringe samplers without introducing headspace. The ROV's screw drive was used to squeeze the water into receiving syringes to maximally retain dissolved gases. Total DIC was analyzed by the Teflon-membrane flow injection method of Hall and Aller (1992), in which the sipper tube was inserted through the three-way valve and the syringe plunger used to prevent formation of headspace during injection. For deep samples from Stevenson Island, unavoidable degassing effects were reduced by shaking the syringe thoroughly just before sipping, as the method measures all forms of CO2 including dissolved gas. Reduced sulfur compounds (hydrogen sulfide, thiosulfate, sulfite) were quantified by a scaled-up modification of the microbore high-performance liquid chromatographic (HPLC) method of Vairavamurthy and Mopper (1990), using dithio-bis-nitropyridine (DTNP) derivatization. Samples were collected in PP syringes and after rinsing, exactly 10 mL were squeezed through 0.2 μm nylon syringe filters (Whatman Acrodisc) into acid-washed 20 mL liquid scintillation vials (LSV). Using a positive displacement repeating pipette, the DTNP reagent was added, the vial capped with a cone-seal cap, and mixed vigorously before storing in a cooler with ice. After return to the laboratory, the precipitated unreacted DTNP was removed with another syringe and nylon filter during injection into the 100-μL HPLC sample loop. Each analysis required 45 min in a dual mobile phase gradient separation on a 250-mm C18 5 μm HS reversed phase column (Alltech Assoc.) so as many as 30 samples could be analyzed daily. Light and dark CO2 incorporation rates were determined by measuring the biological conversion of acid-labile 14C-bicarbonate into acid-stable organic 14C, as described previously (Cuhel et al., 2002). Briefly, suitable aliquots of fresh vent water or lake samples, usually 180 mL, were dispensed with minimal mixing into an acid-washed PP beaker. Enough high specific activity 14C-bicarbonate (56 mCi mmol−1, MP Biomedical) was added to give about 2 × 106 DPM mL−1. The sample was drawn into a positive displacement 50 mL repeating pipette tip, and 10 mL aliquots were gently added to acid-washed 20 mL LSV in custom machined aluminum incubator blocks. Additions (thiosulfate, inhibitors, other stimulants, etc.) had been previously loaded into the appropriate vials at 1:100 to 1:1000× dilution from concentrated stocks. Temperature was controlled by a water bath circulator through the large 64-place block for 15°C incubations with triplicates and many treatments. Photosynthesis was measured identically, except that the projector lamp light source (ELH, 4 × 300 W) was turned on and incubations spanned only 3 h. Elevated temperature incubation (controls, +thiosulfate in duplicate only) was accomplished in electrically heated aluminum dry block incubators. In these, 10 mL of sample were heated from ambient to 80°C in about 11 min during a ~12 h incubation, minimizing artifacts of transient temperature increases in the upper mesophilic range. All vials were capped with cone-seal caps to reduce loss of volatile species, while the atmospheric oxygen contained in 12 mL of headspace guaranteed aerobic conditions for the measurements (>4 mM dissolved oxygen equivalents). Anaerobic chemosynthesis assays were beyond the capabilities of the field laboratory. For practical reasons, most incubations were initiated in late evening after field sampling and sample processing, and terminated prior to the next morning's ROV expedition, usually 10–14 h of incubation. Each measurement was terminated by injection of 0.25 mL 2 N H2SO4 followed by >12 h shaking (100 RPM) to remove unmetabolized 14C, addition of liquid scintillation cocktail (Hydrofluor; National Diagnostics), and storage until counting. Duplicate 10 mL aliquots for background 14C contamination were shot into acid-containing LSV immediately after dispensing block samples; in 2003 these typically yielded 10 relative to lake water (Table 1), and were likely to have deep geothermal fluid sources; this interpretation is supported by previous porewater analyses from hydrothermally active sediments of Mary Bay and West Thumb that had yielded very high chloride concentrations, near 4–9 mM at 30 cm sediment depth (Aguilar et al., 2002). Thus, the localized high concentrations of ammonia, DIC, and sulfide at these two vents at least in part represented deeply sourced chemical species. Interestingly, the deep and hot Stevenson Island 72 sample showed no selective chloride or silicate enrichment that unequivocally distinguishes deep geothermal fluid sources. The high concentrations of sulfide, DIC, and ammonia may arise through transport in subsurface conduits as gases in the steam phase rather than as dissolved ionic species. The samples Mary Bay West 12 and West Thumb 98 showed the lowest sulfide, DIC, ammonia, and nitrate concentrations, and no conservative marker signature (chloride, silicate) of deeply sourced geothermal fluids; the shallow West Thumb 98 sample showed no chemical enrichment of any parameter besides sulfite (Table 1). Dissolved organic carbon (DOC) was poorly related to physical–chemical variables and likely derived from lake water admixture at vent orifices. Nitrate, an important substrate for anaerobic respiration, was virtually absent in Yellowstone Lake waters. During the 2003 season, 133 water samples, including 69 from hydrothermal vents, were analyzed for nitrate. Only 13 samples, 10 of these in the Stevenson Island domain, had nitrate concentrations above 0.5 μM; none exceeded 2 μM. Chemosynthetic Activity The vent water samples showed distinct, temperature-dependent patterns of dark CO2 fixation (Figure 1). The addition of the bacterial protein synthesis inhibitor chloramphenicol reduced chemosynthetic activity, whereas the eukaryotic protein synthesis inhibitor cycloheximide did not affect chemosynthesis rates (data not shown). Biomass nutrient elements N and P were sufficient to support chemosynthesis at the level of electron donors available in these measurements. Figure 1. Dark carbon dioxide fixation by Yellowstone Lake hydrothermal vent samples measured in triplicate (15°C) or duplicate incubations (50, 60, and 80°C) with (+S) or without addition of 5 mM thiosulfate. Biological fixation controls with added S + 20 μg/mL chloramphenicol (SC) were tested at 15°C only. UD, undetectable (10×) at 50°C but was associated with very high replicate error for 60°C incubations. Because the replicates for almost all other incubations agreed to a few percent, it is likely that the West Thumb 129 sample contained bacteria either clumped or attached to particles with patchy distribution. The positive dark fixation results at 50 and/or 60°C in Mary Bay, West Thumb 129, and Stevenson Island 72 strongly implicate chemosynthetic activity by thermophilic autotrophs in these samples. Chemosynthetic activity in the mesophilic range at 15°C was low at West Thumb 129 and Stevenson Island 72 (below 0.02 μM C h−1), indicating mesophilic autotrophs in reduced numbers or activity compared to the Mary Bay samples. West Thumb 129 was the only sample that showed low but detectable chemosynthetic activity at 80°C, indicating the existence of hyperthermophiles. The West Thumb 98 sample showed very low dark CO2 fixation rates close to the detection limit and the lake water background, generally below 0.002 μM C h−1 for all temperatures; a low but detectable rate near 0.028 μM C h−1 was obtained for thiosulfate-amended water at 50°C (Figure 1). The distinct temperature effects on chemosynthetic activity suggest the existence of two groups of chemosynthetic microorganisms: chemosynthetic mesophiles in the two Mary Bay Samples, and thermophiles in the Mary Bay Canyon 28, West Thumb Canyon 129, and Stevenson Island 72 samples. The Mary Bay Canyon 28 sample likely contained both types of chemosynthetic communities. The nearly inactive West Thumb 98 sample should contain few detectable chemoautotrophs, although seed populations might be present that account for low-level thermophilic sulfur stimulation. These inferences are consistent with the results of previous sampling surveys. During a previous 3-year sampling period of 1997, 1998, and 1999, Mary Bay water samples showed the highest sulfide concentrations (max. 0.7–0.8 mM), the highest DIC concentrations (max. 16–17 mM), and also the highest dark CO2 fixation rates (max. 0.3–0.6 μM C h−1) at mesophilic temperatures, in comparison to significantly lower concentrations and rates found in Stevenson Island and West Thumb water samples (Cuhel et al., 2002). Thus, previous studies also suggest the existence of mesophilic, chemosynthetic microbial communities in Mary Bay. Photosynthetic Activity Photosynthesis-irradiance curves for surface samples from the three domains of Mary Bay, Stevenson Island, and West Thumb demonstrated light-saturable photosynthetic CO2 fixation (Figure 2). Light stimulated photosynthetic rates to 200 μmol PAR photons m−2 s−1, about 10% of full sunlight, above which rates remained constant at 0.14 ± 0.01 μM C h−1. Because this discussion concerns volumetric carbon fixation, the data were not normalized for varying algal biomass as chlorophyll a and are presented in the same units as chemosynthesis for direct comparison. Figure 2. Photosynthesis-irradiance relationships at 15°C for surface waters overlying hydrothermal vent fields in Mary Bay (●), Stevenson Island (■), and West Thumb (▲). Consistent with the working hypotheses based on temperature-sensitive chemosynthetic rates, the clone libraries from the five sampling locations show distinct microbial community compositions (Table 1). The clone libraries from the two samples with the highest temperatures, West Thumb Canyon 129 and Stevenson Island 72, consistently cluster together in Principal Component analysis based on shared 16S rRNA phylotypes (Figure 3). The clone libraries for the other sites did not show any correlations, a possible consequence of data set size but also evident from deeply divergent microbial community composition (Table 1). Figure 3. Principal component analysis plots showing the clustering of 16S rRNA clone libraries based on shared OTUs, weighted for abundance. Each axis indicates the fraction of the variance in the data that the axis accounts for. The first and the second Principal Component explain most of the data (P1 = 41.4, P2 = 30, P3 = 17.8%). The Mary Bay West 12 sample, from an active bubbling vent near the lake shore, was dominated by gammaproteobacterial phylotypes related to the mesophilic sulfur oxidizer Thiovirga sulfuroxydans; this bacterium has an optimal growth temperature of 30–34°C (total growth range 15–42°C), and grows as an obligate chemolithoautotroph by oxidizing sulfur, sulfide, and thiosulfate aerobically; its 16S rRNA gene sequence forms a monophyletic lineage with very similar (at least 97% similarity) phylotypes from sulfidic and geothermal waters (Ito et al., 2005). The Mary Bay West 12 sample also yielded clones related to a betaproteobacterial cluster from diverse freshwater environments that included the freshwater bacteria Variovorax and Rhodoferax (Table 1; Figure 4). This betaproteobacterial cluster is generally found in freshwater environments, and has a cosmopolitan distribution (Zwart et al., 2002). The Mary Bay Canyon 28 sample harbored Thiovirga-related clones as well, but its bacterial community appeared to be differently structured and consisted at least in part of clones related to anaerobic bacteria (Table 1); no PCA clustering of the two Mary Bay samples was observed (Figure 3). Several clones were affiliated with anaerobic Deltaproteobacteria that usually occur in aquatic sediments but not in the water column; these include sulfate-reducing bacteria of the Desulfobacteraceae, with the butyrate oxidizer Desulfatirhabdium butyrativorans as the closest match (Balk et al., 2008); the heterotrophic halorespiring bacterium Anaeromyxobacter dehalogenans (Sanford et al., 2002); and uncultured bacteria from the sediment of an eutrophic lake. No other water sample yielded deltaproteobacterial clones. Also, Mary Bay West 28 contained close relatives of the anaerobic, nitrate-reducing and sulfur-oxidizing autotrophic bacterium Thiobacillus denitrificans within the Betaproteobacteria, and of the facultatively anaerobic, microaerophilic, or nitrate-reducing sulfur oxidizer Sulfuricurvum kujiense within the Epsilonproteobacteria (Kodama and Watanabe, 2004; Figure 4). This distinct microbial community signature corresponded to a different setting. Mary Bay 12 was a bubbler in shallow open water at low temperature (15°C) and high mixing rate, which never exceeded 20°C and was near freezing for 6 months of the year. In contrast, the hot Mary Bay Canyon 28 sample (49°C at sampling), the most confined of all the sample locations, came from the bottom of a canyon-like crater at ca. 56 m depth, with nearby sediments hot enough to melt a core liner. With a sill depth of 20 m, these steep-walled hydrothermal explosion craters are characteristic for Mary Bay (Morgan et al., 2003b) and provide more geochemically favorable conditions for anaerobic, especially heterotrophic bacterial growth. The conspicuous sequence signature of obligately or facultatively anaerobic bacteria may indicate deep-growing populations from hydrothermal sediments at the bottom of the crater that undergo upward advection and suspension within into the deep-water layers of this enclosed basin. Figure 4. Phylogeny of Mary Bay West 12 and Mary Bay Canyon 28 proteobacterial clones, based on E. coli 16S rRNA gene nucleotide positions 723–1491. In addition, Mary Bay Canyon 28 harbored a clone most closely related to the autotrophic iron-oxidizing bacterium Gallionella ferruginea, and two clones of the thermophilic, chemosynthetic phylum Aquificales, specifically the hydrogen- and sulfur-oxidizing genus Sulfurihydrogenibium (Figure 4). Thus, Mary Bay Canyon 28 contains an unusually multifaceted microbial community, consisting of mesophilic and thermophilic chemosynthetic bacteria within the Beta-, Gamma-, and Epsilonproteobacteria and the Aquificales (consistent with high chemosynthetic rates at both temperature regimes), as well as nitrate- and sulfate-reducing anaerobes. The microbial community of the deep, hot Stevenson Island 72 sample was distinct from those of both Mary Bay samples. Almost half of the cloned 16S rRNA gene sequences grouped with the Aquificales (Table 1) and are most closely related to clones from other Yellowstone Park locations (Figure 5) and the cultured strain Sulfurihydrogenibium spp. YO3AOP1 from Obsidian Pool in Yellowstone National Park (Reysenbach et al., 2009). These populations were likely from the vent throat or orifice near deep lake water; the thermistor on the sampling arm of the ROV gave 110°C, indicating source fluid temperatures possibly above 125°C. The temperature optimum of cultured Sulfurihydrogenibium strains and species is between 65 and 70°C; depending on the species, growth is possible between 40 and 78°C (Nakagawa et al., 2005). The species most closely related to the Yellowstone Lake clones, Sulfurihydrogenibium yellowstonense strain SS-5, has a growth temperature range of 55–78, 5–8°C more tolerant of high temperatures than other described species (Nakagawa et al., 2005); it uses sulfur and thiosulfate but not hydrogen as electron donors, and is obligately aerobic; it assimilates organic carbon compounds for biosynthetic purposes, but is unable to use them as energy sources (Nakagawa et al., 2005). Other phylum-level bacterial groups in the Stevenson Island sample included Betaproteobacteria, Actinobacteria, Planctomycetales, and Verrucomicrobia, plus a single Thiovirga-related gammaproteobacterial clone (Table 1). Figure 5. Phylogeny of Stevenson Island 72 bacterial clones, based on E. coli 16S rRNA gene nucleotide positions 25–1491. The microbial communities of the Stevenson Island 72 and West Thumb Canyon 129 resembled each other, as confirmed by clustering in PCA analysis (Figure 3). West Thumb Canyon 129 had the next-highest temperature (77°C) after the Stevenson Island sample; both samples shared abundant Aquificales clones specifically related to the cultured species of the genus Sulfurihydrogenibium, and to Sulfurihydrogenibium-related clones from different locations within Yellowstone National Park (Figure 6). The abundance of Sulfurihydrogenibium clones is consistent with the high sulfur-stimulated chemosynthetic rates at 60°C, and the lower but still substantial rates at 50°C in these two samples (Figure 1). Since chemosynthesis rates and sulfur stimulation persisted at 80°C at West Thumb Canyon 129 (Figure 1), it is possible that this sample contained high-temperature-adapted strains of Sulfurihydrogenibium, or different types of thermophiles and hyperthermophiles that remain to be found. Next to the Aquificales, the most frequently recovered clones represent Betaproteobacteria and Actinobacteria, which occur in the West Thumb Canyon 129, Stevenson Island 72, Mary Bay West 12, and (to a lesser extent, only Betaproteobacteria) the Mary Bay Canyon 28 samples (Table 1). Figure 6. Phylogeny of West Thumb Canyon 129 bacterial clones, based on E. coli gene nucleotide positions 25–573. The West Thumb Canyon 129 sample also contained, in similar abundance, phylotypes of the Chloroflexi and the Thermodesulfovibrio lineages; the latter was not found in other clone libraries (Table 1), potentially a result of terrestrial spring influx limited to the West Thumb region. Within the Thermodesulfovibrio lineage, the phylotypes from West Thumb Canyon 129 were most closely related to the autotrophic, hydrogen-oxidizing, iron-reducing bacterium Geothermobacterium ferrireducens (Figure 6) previously isolated from hot spring sediments in Yellowstone National Park (Kashefi et al., 2002). The West Thumb area harbors a suitable biogeochemical niche for this bacterium: iron-manganese oxide crusts were found on the hydrothermally active lake bottom, and the upper sediment layers contain porewater concentrations of 20–40 μM dissolved, reduced iron (Aguilar et al., 2002). The fifth sample, a relatively cool West Thumb 98 sample with low chemosynthetic activity, yielded no Aquificales or other chemosynthetic bacterial populations, but predominantly members of the Actinobacteria (Figure 7) and the Betaproteobacteria (Figure 8), the bacterial community components that occur to some extent in all Yellowstone Lake water samples (Table 1). The actinobacterial clones in this and other Yellowstone Lake samples are members of uncultured Actinobacterial freshwater lineages with a cosmopolitan distribution, the acI and acIV clusters (Warnecke et al., 2004). In subsequent sequencing surveys of freshwater lakes, 16S rRNA genes of these clusters were found very frequently and in high diversity. The clades were further subdivided into clades AI to AVII for the acI linage (Newton et al., 2007) and clades acIV-A to acIV-E for the acIV lineage (Warnecke et al., 2004; Holmfeldt et al., 2009); this nomenclature is followed in phylogenetic trees in this study. Actinobacterial acI or acIV clades were found in almost every water sample, Mary Bay 12 (Figure 9), Stevenson Island 72 (Figure 5), West Thumb Canyon 129 (Figure 6), and West Thumb 98 (Figure 7), and most likely represent the admixture of Yellowstone Lake water and its indigenous microbial community to the thermal water samples. Since acI and acIV strains have not been cultured yet, a physiological rationale for the occurrence of these bacteria in Yellowstone Lake water is hard to infer. Interestingly, comparative quantifications of the acI clade in high mountains lakes have identified UV irradiation as a potential factor selecting for acI actinobacteria (Warnecke et al., 2005). Figure 7. Phylogeny of West Thumb 98 bacteria except Proteobacteria, based on E. coli 16S rRNA gene nucleotide positions 25–1491. Figure 8. Phylogeny of West Thumb 98 proteobacterial clones, based on E. coli 16S rRNA gene nucleotide positions 25–1491. Figure 9. Phylogeny of Mary Bay West 12 and Mary Bay Canyon 28 bacterial clones, except Proteobacteria, based on E. coli 16S rRNA gene nucleotide positions 723–1491. The results from the Yellowstone Lake hydrothermal vents form an interesting contrast to previous results from multiple aerial hot springs in Yellowstone National Park (Spear et al., 2005). By combining chemical analysis of spring waters for electron donors including sulfide and hydrogen, thermodynamic modeling of energy yields from the aerobic oxidation of these electron donors, and extensive 16S rRNA gene sequencing, aerobic hydrogen oxidation was identified as the favored energy source in Yellowstone hot springs, consistent with 16S rRNA gene clone libraries dominated by hydrogenotrophic genera of the Aquificales, such as Hydrogenothermus, Hydrogenobacter, and Hydrogenobaculum (Spear et al., 2005). Close relatives of mesophilic sulfur-oxidizing bacteria (Thiovirga spp.) occur in some locations, for example in the Mary Bay sampling sites, and most likely contribute to dark CO2 fixation rates measured at cool temperatures. Consistent with these results, previous studies have shown that dark CO2 fixation rates at Mary Bay locations are strongly stimulated by thiosulfate enrichment (Cuhel et al., 2002). In contrast, clone library results from the hot Stevenson Island and West Thumb Canyon vents, show that mesophilic sulfur oxidizers such as Thiovirga spp. are not detected in these habitats, or occur only as a minority. Here, the spectrum of clones changes toward phylotypes that are most closely related to thermophilic and hyperthermophilic chemolithoautotrophs of the genus Sulfurihydrogenibium that use sulfur and hydrogen as electron donors. As a caveat, S. yellowstonense, the closest relative to the Yellowstone Lake clones in this dataset, oxidizes sulfur and thiosulfate, but not hydrogen. Since chemolithoautotrophic microorganisms may use one or several different electron donors, including reduced sulfur compounds such as H2S, polythionates, Fe(II), Mn(II), NH3, or H2, our results have obvious limitations. Here, thiosulfate () was chosen as model reduced sulfur stimulant of chemosynthesis because it does not as easily react with other substrates as might have happened with H2S as a supplement. Since thiosulfate was rarely found in quantity even when H2S was abundant (Table 1), it was most likely utilized rapidly upon (a)biotic production from sulfide. Thiosulfate-stimulated autotrophic CO2 fixation implicated the presence of bacteria capable of using it, and possibly other reduced sulfur compounds, as electron donors. A lack of thiosulfate stimulation would imply either electron donor saturation, or the absence of thiosulfate-oxidizing bacteria. Interestingly, thermophilic dark CO2 fixation rates at Mary Bay Cayon 28 and Stevenson Island 72 were reduced by ca. 10% after thiosulfate addition (Figure 1); reactions of the added thiosulfate (or its disproportionation products) with other electron donors such as Fe(II), might reduce their availability, and thus reduce the autotrophic contribution of non-sulfur lithotrophs. Nitrate Reduction and Metal Reduction The chemosynthesis rates in this study were measured aerobically, assuming that chemosynthetic microbial communities venting into a well-oxygenated oligotrophic lake would respire with oxygen. The prevalence of 16S rRNA gene sequences related to aerobic chemosynthetic bacteria (Thiovirga, Aquificales) supports this assumption. Niches certainly exist for anaerobic, nitrate- and metal-reducing chemosynthesis in Lake Yellowstone, for example anaerobic vent fluid, sediments or hydrothermal mineral deposits. Very low oxygen solubility at high temperature, and the presence of reducing compounds including Fe(II) and H2S, might facilitate anoxic conditions in vent source waters and possibly during channelized flow toward the lake-bottom orifice. As a result, phylotypes related to anaerobic chemosynthetic bacteria, such as the nitrate-reducing sulfur oxidizers Thiobacillus denitrificans and Sulfuricurvum kujiense, or the iron-reducing hydrogenotroph Geothermobacterium ferrireducens, were detected as well. Because 16S rRNA genes related to nitrate-reducing sulfur oxidizers were detected in Mary Bay 28, this deep, stratified canyon represents a likely habitat where nitrate-respiring vent or sediment populations accumulate to sufficient densities to be detected in clone libraries; such microbial nitrate sinks could compound the functional absence of nitrate (usually

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