Yellowstone Science

volume 18 • issue 3 • 2010

Recording Change at Mammoth Hot Springs

Microbial Diversity from Harsh Environments

ANA HOUSEAL

"We cannot create observers by saying 'observe,' but by giving them the power and the means for this observation, and these means are procured through education of the senses."

—Maria Montessori,
Italian physician and educator

The Power of Observation

I remember visiting Mammoth Hot Springs during my family's trip to Yellowstone when I was in elementary school. For me, the terraces paled in comparison to the excitement of the geysers, the vivid colors of hot pools, and the surprise of seeing wildlife species we had never seen before. Having observed the Mammoth terraces now over many years, I've concluded that a single visit is interesting, but only after multiple visits can you begin to appreciate how dynamic the area really is.

In this issue, Ana Houseal shares a project in which elementary and junior high school students work with teachers and scientists to capture photographs and data that record often dramatic changes at the terraces over time. These students are creating a database that will be available for future study while learning valuable lessons about the power of observation and the scientific process. Maybe one of them will go on someday to be involved in a project like Brett Carr's, where scientists are using aerial photographs and modern technology to map changes at Mammoth and measure thermal water discharge from the system. Maybe one of them will choose to study the park's extreme thermophiles, as discussed by Dennis Grogan in his article. And hopefully all of them will leave the park with a deeper understanding of and appreciation for a system that, at first glance, seems quiet and simple.

I hope you enjoy the issue.

Yellowstone Science

a periodical devoted to
natural and cultural resources

volume 18 • issue 3 • November 2010

Tami Blackford
Editor
Graphic Designer

Mary Ann Franke
Associate Editor

Janine Waller
Assistant Editor

Emily Yost
Assistant Editor

Artcraft Printers, Inc.
Bozeman, Montana
Printer

Yellowstone Science is published periodically. Support for *Yellowstone Science* is provided by the Yellowstone Association, a nonprofit educational organization dedicated to serving the park and its visitors. For more information about the association, including membership, or to donate to the production of *Yellowstone Science*, visit www.yellowstoneassociation.org or write: Yellowstone Association, PO Box117, Yellowstone National Park, WY 82190. The opinions expressed in *Yellowstone Science* are the authors' and may not reflect either National Park Service policy or the views of the Yellowstone Center for Resources.

Copyright © 2010, Yellowstone Association for Natural Science, History & Education.

For back issues of *Yellowstone Science*, please see www.greateryellowstonescience.org/ys.

Submissions are welcome from all investigators conducting formal research in the Yellowstone area. To submit proposals for articles, to subscribe, or to send a letter to the editor, please write to the following address: Editor, *Yellowstone Science*, PO Box 168, Yellowstone National Park, WY 82190. You may also email: yell_science@nps.gov.

Yellowstone Science is printed on recycled paper with a soy-based ink.

Cover photo:
Canary Spring at Mammoth Hot Springs: *top* July 18, 2008, *bottom* May 3, 2009. Courtesy Ana Houseal.

Mammoth Hot Springs, one of the most rapidly and dramatically changing sites in Yellowstone National Park, April 20, 2009. STaRRS photo point 9.

FEATURES

DEPARTMENTS

News & Notes


PAUL SCHULLERY

The new Old Faithful Visitor Education Center.

Old Faithful Visitor Education Center Opens

On August 25, 2010, a dedication ceremony and grand opening was held at the new Visitor Education Center at Old Faithful in Yellowstone National Park. It was hosted by Yellowstone Superintendent Suzanne Lewis, and author and former Yellowstone historian Paul Schullery gave the keynote address. Assistant Secretary of the Interior for Fish, Wildlife and Parks Tom Strickland, director of the National Park Service Jon Jarvis, and chairman of the Yellowstone Park Foundation Bannus Hudson also offered remarks.

The event opened with music from the Wyoming National Guard's 67th Army Band and presentation of the colors by the Yellowstone National Park Mounted Color Guard. At the end of the ceremony the building opened to the public, offering visitors access to the interactive exhibits, including a working model geyser.

The building was designed to set new standards for accessibility and for the interpretation of complex scientific information to the public. It is one of the first National Park Service visitor centers to achieve Gold LEED certification from the US Green Building Council in recognition of its sustainable construction and operational standards.

Of the $27 million design and construction cost of the new building, $15 million was provided by the nonprofit Yellowstone Park Foundation, the official fundraising partner of Yellowstone National Park. More than 400 individuals, foundations, and corporations made contributions to the Yellowstone Park Foundation for the project. These contributions ranged from $2.00 to $3 million.

Superintendent Suzanne Lewis Retires

After nearly 32 years in the National Park Service, Yellowstone Superintendent Suzanne Lewis retired on October 22, 2010. As superintendent since February 10, 2002, she managed more than 2.2 million acres, a staff of 800, and an annual base budget of more than $36 million.

She began her National Park Service career as a seasonal park ranger in 1978 at Gulf Islands National Seashore. During her 11-year tenure there, she served in a variety of positions including park technician, park historian, supervisory park ranger, and management assistant to the superintendent. Chosen in 1988 for an international assignment to the Republic of Haiti, she assisted the United Nation's efforts to preserve, protect, and educate Haitians in the preservation of natural and cultural resources. In 1989, Lewis was appointed acting superintendent of Christiansted National Historic Site and Buck Island Reef National Monument. In 1990, she was selected as the first superintendent for the newly created Timucuan Ecological and Historic Preserve. Lewis served as the superintendent for the Chattahoochee River National Recreation Area from 1997 to April 2000. She was superintendent at Glacier National Park prior to her Yellowstone appointment.

Lewis earned her BA (magna cum laude) in American History in 1978 from the University of West Florida. During her Senior Executive Service Candidate Development Program, she completed assignments with the Department of Interior Secretary's Special Assistant for Alaska, the Department of Interior Office of Management and Budget, the Walt Disney World Corporation, Harvard University, and Carnegie Mellon University.

Lewis received numerous awards throughout her National Park Service career, including the Rachel M. Carson Award for Women in Conservation from the National Audubon Society (2010), the Presidential Rank Award for Senior Executives in government (2009), a National Women's History Month Honoree (2007), the Secretary's Bronze Executive Leadership Award (2004), the National Park Service Meritorious Service Award (2003), and the National Parks and Conservation Association Park Manager of the Year for Partnerships (1994). She was also awarded the Woman of Distinction Award by the Girl Scout Councils of America in 1997.

Questioning Greater Yellowstone's Future
Climate, Land Use, and Invasive Species

The 10th Biennial Scientific Conference on the Greater Yellowstone Ecosystem

Summary of the 10th Biennial Scientific Conference on the Greater Yellowstone Ecosystem

Approximately 200 agency managers, scientists, and university researchers and students joined together October 11–13, 2010, to participate in the *Questioning Greater Yellowstone's Future: Climate, Land Use, and Invasive Species* conference held in Yellowstone National Park, Wyoming, at the Mammoth Hot Springs Hotel. The goal of this conference was to generate discussion on changes in three ecological drivers—climate, land use, and invasive species—that could dramatically alter Greater Yellowstone's public and private lands. This conference offered participants an opportunity to help shape this region's understanding of key issues such as how regional climate may change in the near future, ecological changes already attributed to changing climate and land use, impacts of increasing demands on public and private lands, threats by nonnative species, and tools and strategies required to address the challenges related to these environmental drivers.

The conference began Monday evening with an opening keynote speech by US Geological Survey (USGS) Director Marcia McNutt. McNutt addressed the USGS's emphasis on an ecosystem approach to natural science and the importance of partnerships to ecosystem restoration. She concluded, quoting Theodore Roosevelt, "The nation behaves well if it treats the natural resources as assets which it must turn over to the next generation increased, and not impaired, in value."

On Tuesday morning, a panel discussion was conducted on the Greater Yellowstone Area (GYA) Science Agenda Workshop held in November 2009, which approximately 90 land managers and experts attended (see *Yellowstone Science* volume 18, issue 2). The panel with Tom Olliff, National Park Service landscape coordinator for the Great Northern Landscape Conservation Cooperative (LCC); Cathy Whitlock, professor at Montana State University; and Yvette Converse, interim coordinator of the Great Northern LCC, discussed the science and strategies identified at the workshop that are intended to drive ecosystem management in the GYA over the next 10–20 years. Converse gave an overview of LCCs and how they may help align conservation programs to work collaboratively towards common landscape goals. The panelists noted that research on the impacts of climate change on cultural heritage and social science studies are needed.

More than 45 presentations were given at the conference during concurrent sessions in addition to the keynote speeches. Session topics included changes in climate, disease, vegetation, wildlife, and aquatic resources; simulation models and technology; trophic cascades; and human adaptations to and alterations of their environment.

Keynote speeches addressed each of the drivers of ecological change in the GYA: climate, land use, and invasive species. Stephen Gray, Wyoming State Climatologist and director of the Wyoming Water Resources Data System, delivered the climate keynote. Gray addressed outcomes of future climate and change in the GYA under different scenarios. He also discussed potential challenges to management and suggested managers maintain and improve monitoring and build capacity for rapid data and information transfer.

Andrew Hansen, professor at Montana State University, gave a keynote on changes in the landscape and land use in the GYA. Hansen discussed what the GYA might look like in the future, and the effects of land use change on biodiversity and other aspects of the ecosystem. He noted that in the past, the wilderness character of the GYA was undesirable to most people and kept the population low. This character is now a major driver of population growth and increased land use intensity. The increased development and population may eventually

NPS/JIM PEACO

Superintendent's International Luncheon speaker Göran Ericsson.

NPS

There were approximately 200 participants at the conference.

adversely impact the very character that is driving that growth. Hansen concluded that creative approaches are needed to sustain the natural amenity-based ecosystem coupled with the natural human system.

Robert Gresswell of the USGS Northern Rocky Mountain Science Center delivered the invasive species keynote. He focused on the Yellowstone cutthroat trout populations in Yellowstone Lake and their significant decline under the illegal introduction of invasive lake trout. Gresswell presented the recommendations of a panel of scientists assembled in 2008 to review Yellowstone National Park's lake trout removal efforts. He stressed that the issue of cutthroat preservation and restoration should be a top priority for area managers. The panel's recommendations were to significantly intensify lake trout removal efforts and invest additional resources in more precise monitoring of lake trout density and spawning behavior.

On Tuesday night, retired National Park Service and USGS biologist Mary Meagher delivered the A. Starker Leopold Lecture, chronicling Yellowstone's range history from management to ecology. Her narrative began in the mid-19th century, before Yellowstone National Park's inception and continued through the beginning of the era of "natural regulation" in the later part of the 20th century. She discussed the many ways that managers and citizens have conceived of wildlife in the Greater Yellowstone area throughout that time and the complex relationships we have had to the wildlife and habitat under our protection.

Professor Göran Ericsson of the Swedish University of Agricultural Science presented the Superintendent's International Lecture on Tuesday afternoon. Ericsson discussed his research on the long coexistence between moose and humans under varying climatic conditions. Moose have adapted to changing climate for more than 6,000 years in Arctic Sweden.

The Aubrey L. Haines Lecture was delivered by Judith Meyer of Missouri State University. Meyer tied historical analysis to scientific analysis, using Yellowstone to demonstrate the connection. She noted, "If Yellowstone's historical record can shed light on the current situation [of science and management], one ray of hope shining from the past might be that Yellowstone has a capacity for infecting its public with a curiosity for science and scientific endeavors, a love and respect for tradition, and with a sense of social responsibility to protect and preserve this place."

Numerous sponsors and partners contributed to the *Questioning Greater Yellowstone's Future* conference: USGS, Northern Rocky Mountain Science Center; US Fish and Wildlife Service; Montana State University; Yellowstone Association; University of Wyoming Ruckelshaus Institute; Rocky Mountains Cooperative Ecosystem Studies Unit; University of Wyoming-National Park Service Research Center; Greater Yellowstone Coordinating Committee: National Park Service (Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, Yellowstone National Park), US Fish and Wildlife Service (National Elk Refuge, Red Rock Lakes National Wildlife Refuge), US Forest Service (Beaverhead-Deerlodge National Forest, Bridger-Teton National Forest, Caribou-Targhee National Forest, Custer National Forest, Gallatin National Forest, Shoshone National Forest); Canon U.S.A., Inc.; Yellowstone Park Foundation; and Greater Yellowstone Science Learning Center. It was planned and organized by the Science Communication Office of the Yellowstone Center for Resources, Yellowstone National Park, with other YCR staff, and a program committee of non-Yellowstone federal agency staff and independent scholars. The proceedings should be available at the end of 2011.

YS

NPS

More than 45 papers were presented and 25 posters were displayed.

NPS/HFC COMMISSIONED ART COLLECTION, ARTIST GIL COHEN

Shorts

Biotransformation of Arsenic by a Yellowstone Alga

Qin, J., C.R. Lehr, C. Yuan, X.C. Le, T.R. McDermott, and B.P. Rosen. 2009. Biotransformation of arsenic by a Yellowstone thermoacidophilic eukaryotic alga. *Proceedings of the National Academy of Sciences* 06(13):5213–5217.

Arsenic, which has been used commercially in very small amounts as a weed killer and insecticide, is a common environmental toxin, ranking first on the Superfund list of hazardous substances. Arsenic concentrations are naturally high in some geothermal environments in Yellowstone National Park, and arsenic biogeochemical cycling has been an area of intense research interest in Yellowstone for years.

Having lived with arsenic for eons, nature has developed interesting ways to handle the toxic compound. For example, some bacteria have evolved mechanisms that detoxify arsenic or, more surprisingly, use it to generate cellular energy. Recently, scientists have gathered evidence that some eukaryotes—organisms (including plants and animals) that have more complex cellular structure than bacteria—have adaptive mechanisms too. A recent article co-authored by Yellowstone researcher Dr. Tim McDermott shows that biochemical reactions within the eukaryotic alga modify the arsenic to become less toxic, at which point it is excreted from the organism.

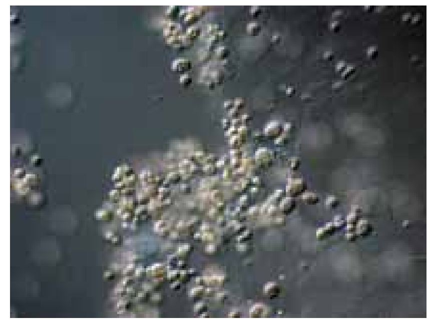
DICK CASTENHOLZ

Enigma type "Galdieria" showing chloroplast in mother and daughter cells.

In Yellowstone, there is a dominant group of algae in the microbial communities of acidic hot springs and heated soils. The green algae mats found in Tantalus Creek running under the boardwalk in Norris Geyser Basin are a good example of this group. These algae are known as *Cyanidioschyon*, *Cyanidium*, and *Galdieria.* They differ from each other in shape and other physiological properties. These algae are different than others in the world in that they thrive in an environment that is very acidic (pH 0.2–3.5) and warm-to-hot (38°C–57°C). No other eukaryotic organism is known to withstand such an environmental extreme, let alone thrive in it. Acidic geothermal environments also contain very high levels of arsenic, and scientists are studying how these tiny plants can tolerate the toxin. The results of these studies are valuable to learning how, for example, agricultural plants might be engineered to avoid the accumulation of arsenic from soils.

Using liquid chromatography and mass spectroscopy, which are analytical chemistry techniques that separate and characterize molecules, the authors found that the Yellowstone alga *Cyanidioschyzon* sp. uses at least two different arsenic detoxification strategies. First, it actively transforms arsenite (the most toxic form of arsenic) to arsenate (a less toxic form) through oxidation. This is similar to what occurs with iron when it forms rust as a result of the addition of oxygen molecules (oxidation) to the iron atoms. Second, the algae modify arsenite by transforming arsenic with hydroxyl groups $[As(OH)_3]$ to arsenic with methyl groups $[As(CH_3)_3]$. Arsenic with methyl groups is highly volatile and excreted by the alga as a gas, which detoxifies the arsenic. The researchers also cloned the genes from the alga that produce the enzyme responsible for the detoxification in order to study the purified enzyme. This led to a breakthrough in the understanding of how the enzyme catalyzes the process of detoxification. Ultimately, this study provides a new view of how these algae function in their environment far beyond photosynthesis, and demonstrates their importance to biogeochemical cycling in hot springs.

—Tim McDermott and Susan Kelly



DICK CASTENHOLZ

Cyanidia.

Remote Measurements of River Channel Depth

Legleiter, C.J., D.A. Roberts, and R.L. Lawrence. 2009. Spectrally based remote sensing of river bathymetry. *Earth Surface Processes and Landforms* 34(8): 1039–1059.

The logistical challenges associated with traditional, field-based methods of characterizing channel form and behavior have restricted stream studies to short, isolated reaches, limiting our ability to understand the organization of river systems at larger spatial and temporal scales. Remote sensing techniques could facilitate progress in fluvial geomorphology, stream ecology, and river management by enabling large-scale, quantitative measurement of various river attributes. This study evaluated the potential for remote measurement of channel depth from optical image data. The researchers used a radiative transfer model to quantify the effects of suspended sediment concentration, variations in bottom reflectance, and water surface roughness; they used ground-based reflectance measurements to assess the accuracy of spectrally-based depth retrieval under field conditions; and they produced depth maps of the Lamar River and Soda Butte Creek from hyperspectral image data consisting of many narrow wavelength bands. This approach was shown to be feasible under conditions where the signal recorded by the remote detector is dominated by radiance reflected from the streambed.

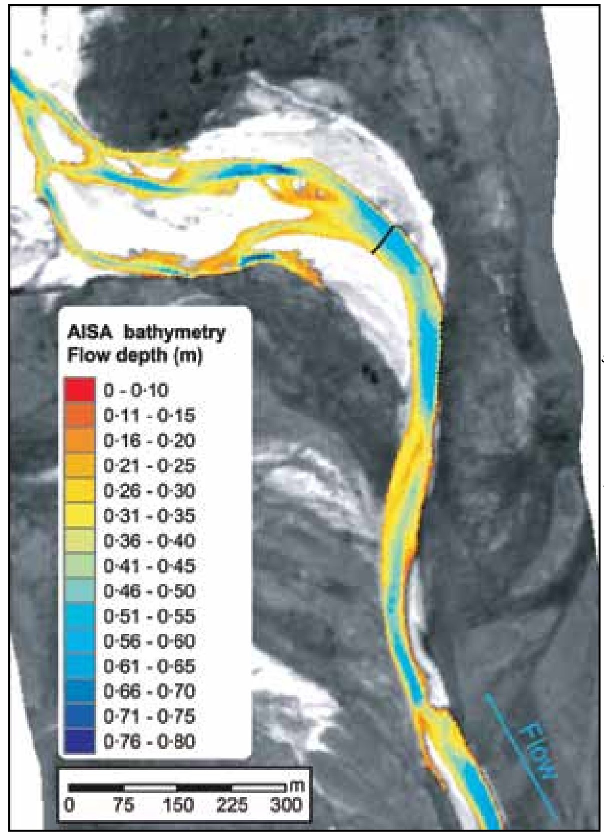
They developed a simple algorithm, Optimal Band Ratio Analysis (OBRA), for identifying pairs of wavelengths that yield strong, linear relationships between an image-derived quantity and flow depth. OBRA of simulated spectra generated by the radiative transfer model indicated that the optical properties of the water column were accounted for by a shorter wavelength numerator band (blue or green) that was sensitive to scattering by suspended sediment, whereas a longer wavelength band (red or near-infrared) subject to strong absorption by pure water provided depth information.

Field spectra collected along Soda Butte Creek indicated that bottom reflectance was fairly homogeneous and that the radiance measured above the water surface was primarily reflected from the bottom, not the water column. Flow depths at spectral measurement locations averaged 27.6 cm and ranged from 4 to 80 cm. OBRA of these data, 28% of which were collected during a period of high turbidity, yielded strong relationships between a spectral band ratio and flow depth, demonstrating that accurate depth retrieval is possible under field conditions. When applied to hyperspectral image data, this approach resulted in spatially coherent, hydraulically reasonable bathymetric maps, and comparison with a subsequent topographic survey suggested that depth estimates were of realistic magnitude. This study indicates that river bathymetry in Yellowstone National Park and similar environments can be accurately mapped using remote sensing.

However, an important difference between field spectra and image data is spatial resolution, which constrains remote mapping of small streams. Reliable depth estimates can be difficult to obtain in very shallow water and along channel banks where pixels include both terrestrial and aquatic features; in the study this juxtaposition of features with very different spectral characteristics resulted in negative depth estimates in some areas. These issues are most pronounced when the image pixel size is an appreciable fraction of the wetted channel width.

—Carl Legleiter

YS



FIGURES REPRINTED WITH PERMISSION OF THE PUBLISHER, JOHN WILEY & SONS, LTD

Spectrally-based map of the Lamar River channel.

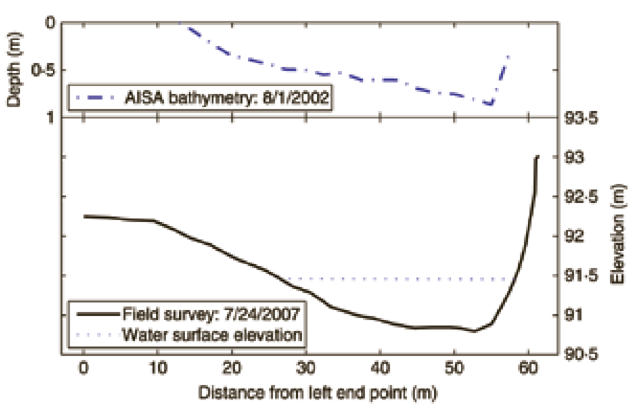


Image-derived depth estimates of the Lamar River channel compared to data from a later topographic survey.

Mammoth Hot Springs

Where change is constant

Ana K. Houseal, Bruce W. Fouke, Robert Sanford, Robert Fuhrmann, and Ellen Petrick

ANA HOUSEAL

STaRRS students get their first panoramic view of New Trail and Canary hot springs, the first stop for photo point data collection on each expedition.

While change is evident in geothermal features throughout Yellowstone, one of the most rapidly and dramatically changing sites in the park is at Mammoth Hot Springs. Visitors to the springs never see the same scenery twice. Even if you are an infrequent visitor, you may notice that the springs seem different each trip. Perhaps the water has changed course, is flowing in a new location, or has ceased to flow altogether. Maybe you notice that the colors seem different than the last time you stood in that spot. Occasionally, you can no longer access a familiar area due to shifts in the springs and the resulting mineral deposition that sometimes engulfs the boardwalk.

The seeming incongruity between memories of favorite springs and their present appearance can be baffling and disorienting. Rangers at the visitor center at Mammoth are veterans at fielding questions such as: "What happened to the hot springs?," "Are they drying up?," or "They sure aren't what they used to be!" The reply is that change is the only constant. The terraces at Mammoth are a direct product of the springs themselves, comprised of calcium carbonate ($CaCO_3$) mineral deposits called travertine that precipitate directly from the hot water (Bargar 1978). While the springs may look very different over time, the total amount of water flowing into and through the entire Mammoth system is relatively constant (Sorey 1991). Yet this has been a difficult concept for visitors to see and, therefore, believe.

To help resolve this "seeing is believing" issue, an integrative Student-Teacher-Scientist Partnership (STSP) was established in 2008 among Yellowstone National Park rangers, university geoscience and education researchers, and a group of 4th to 8th grade teachers and students. The partners work together to answer real-world questions about a phenomenon or problem the scientist is studying (Tinker 1997).

Called STaRRS (Students, Teachers, and Rangers & Research Scientists—Investigating Earth Systems at Mammoth), this STSP was designed to achieve several goals: (1) establish a connection with university researchers so that students in grades 4–8 would develop a deeper understanding of research taking place in Yellowstone; (2) have more year-round observations and data coverage at Mammoth for the university research team; and (3) expand the *Expedition: Yellowstone!* curriculum to include more specific scientific investigations.

The National Park Service established *Expedition: Yellowstone!* in 1985 as a curriculum-based, multi-day education program to provide four- and five-day overnight experiences in the park to investigate natural and cultural resources. For more than two decades participants have gathered pH and temperature data at Mammoth. In addition to the regular curriculum, STaRRS students made observations and collected data on a few key physical, chemical, and biological parameters at strategic sites along the hot spring drainage systems at Mammoth. These sites, called photo points, provided visual data to help park visitors and scientists monitor geothermal change over time.

Use of Mammoth Hot Springs for a scientific and educational partnership

Mammoth Hot Springs has long generated interest for visitors because of its renowned terrace-shaped travertine mineral deposits (Bargar 1978). It provides an exceptional combination of natural and logistical attributes for use as a natural teaching and research laboratory for the STaRRS program.

The effervescent release of carbon dioxide (CO_2) from the spring water results in rapid travertine precipitation (5 mm/day or ¼ in/day), which is composed of the calcium carbonate minerals aragonite and calcite (Fouke et al. 2000; Kandianis et al. 2008). Travertine precipitates in a variety of distinct crystalline shapes and forms that systematically change from upstream to downstream within each drainage flow path (Fouke et al. 2000). Each type of travertine is associated with discrete communities of heat-loving microorganisms (thermophilic bacteria and archaea) that grow in communities referred to as microbial mats and exhibit a wide variety of colors and shapes. They grow even more quickly than the remarkably high rate at which the travertine mineralization takes place (Fouke et al. 2003; Fouke in press). Although there are many travertine-depositing hot springs throughout the world, Mammoth is unique because of the long-term protection from human impacts afforded by the National Park Service. Mammoth has the added benefit of year-round access to the Lower and Upper terrace boardwalks, which provide safe access for visitors, students, and professional groups. Furthermore, its proximity to gateway communities make Mammoth an accessible centerpiece for integrated teaching and research.

The geology of Mammoth Hot Springs

The spring water at Mammoth is derived from rain water and snowmelt that flows from the southern margin of the Gallatin Mountain Range into the deep subsurface along associated fault systems. Estimates of how long it takes water to make this hydrologic transit range from less than 2,000 to more than 11,000 years (Rye and Truesdell 2007). During

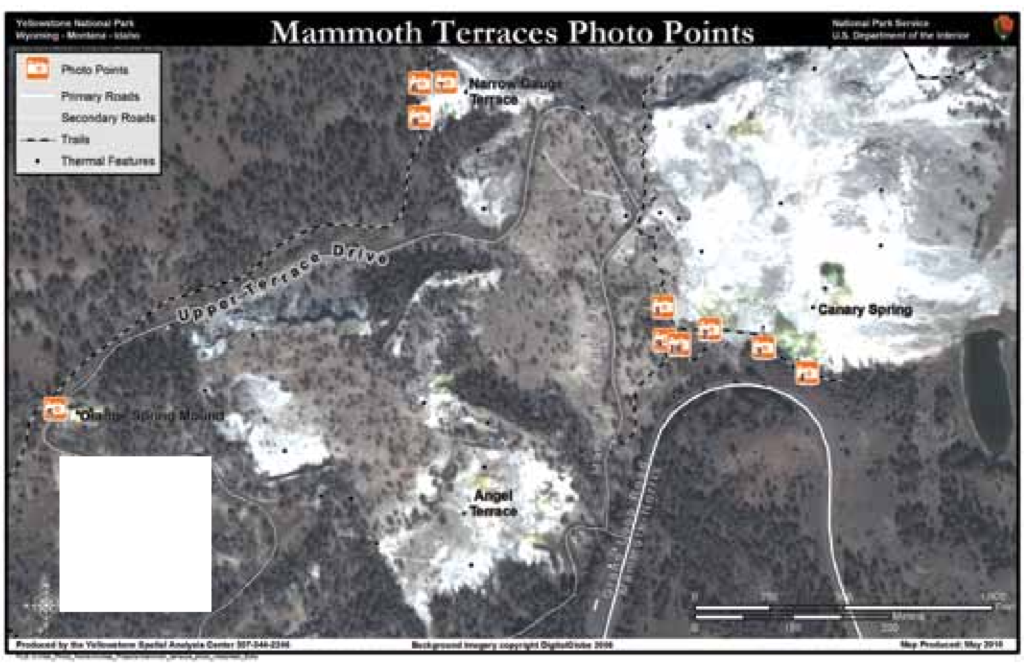


Figure 1. Geographic map of hot springs along the Upper Terrace Loop on the Highland, Angel, and Main terraces at Mammoth Hot Springs. Photo point locations are shown. *Inset:* Location of Mammoth Hot Springs in Yellowstone National Park.

At many locations within the Mammoth complex, as much as one meter of travertine accumulates in a single year.

this travel time, the water flows through and dissolves limestone and evaporite rocks that were deposited approximately 350 million years ago during the Mississippian Period (Sorey 1991). The groundwater is heated to more than 100°C (212°F) by rock heated by the underlying Yellowstone hotspot, which causes it to rise again to the surface through large subsurface fracture systems at Mammoth. During this underground journey, the spring water becomes super saturated with dissolved carbonate minerals and CO_2 gas. The groundwater emerges from the vents at Mammoth at 73°C (163°F) and a neutral pH of 6. The CO_2 immediately degasses from the water, causing a rapid increase in the water's pH and creating conditions favorable for rapid $CaCO_3$ mineral precipitation (Friedman 1971). This process forms the hallmark travertine terraces at Mammoth. The resident bacteria and archaea populations are an important part of this $CaCO_3$ precipitation process, resulting in the long-term accumulation of thick travertine deposits (Kandianis et al. 2008).

At many locations within the Mammoth complex, as much as one meter of travertine accumulates in a single year (Fouke et al. 2000; Kandianis et al. 2008; Veysey and Goldenfeld 2008). In geologic terms this travertine growth occurs at light speed. On average, this is one million to one billion times faster than limestone deposition in most other geological settings, such as the deep sea floor or in caves. In fact, the only reason that travertine has not covered all of Yellowstone is that the flow paths at Mammoth Hot Springs are small and the drainage systems flow in one place for only a relatively short period before switching to another location. Over time, this has formed a succession of travertine limestone deposits at Mammoth and at Gardiner, Montana. The Gardiner travertine ranges in age from approximately 20,000 to 39,000 years old, while the travertine at Mammoth ranges in age from 0 to nearly 8,000 years before present (Sturchio et al. 1992, 1994; Butler 2008; Vescogni 2009). The travertine terraces at Mammoth are 73 meters thick and cover an area more than 4 square kilometers (Allen and Day 1935; White et al. 1975). The terraces at Gardiner, which are now part of a privately-owned quarry, are comparable in size (Sorey 1991).

STARRS PHOTO POINT 5

Orange Spring Mound is the site of photo point 5. It was chosen for both ease of access and recent visible activity.

Systems geobiology research at Mammoth Hot Springs

The systems geobiology research group at the University of Illinois at Urbana-Champaign includes geologists, geochemists, microbial ecologists, genomocists, physicists, and educational specialists. Their research at Mammoth focuses on ways in which the environment influences and controls microbial life, and microbial life influences and alters the environment. Understanding the carbonate rock record and the relationships between the biotic and abiotic components of the hot spring ecosystem can assist in understanding modern and ancient geological landscapes on Earth and potentially other planets. The group's research is producing models of water-mineral-microbe interactions that predict system-scale dynamics across large dimensions of time and space in a wide variety of natural environments around the world.

The Illinois research group developed a model that can effectively track and predict interactions between water, minerals, and microbes that influence travertine deposition (Fouke et al. 2000, 2003; Fouke in press). From this work, four parameters were identified that control travertine deposition: (1) temperature, (2) pH, (3) flow rate and flow dynamics, and (4) system composition—contextual observations of travertine (shape and form), microbial mats (color, shape, size, growth rates), and distance along the drainage system from the source. Since the spring is constantly changing, the location within the hot springs where a particular parameter, such as a change in pH, is observed is also associated with changes in travertine formation and microorganisms (Veysey et al. 2008).

Fouke et al. (2000) developed a model of the hot springs that aids in understanding these complex systems

Facies	Vent	Apron and Channel	Pond	Proximal Slope	Distal Slope
Temp °C	73–71	70–60	59–45	44–35	35–28
pH	6.0	6.1–6.5	6.6–7.2	7.3–7.7	7.8–8.1
Minerals	aragonite	aragonite	aragonite and calcite	aragonite and calcite	calcite

B

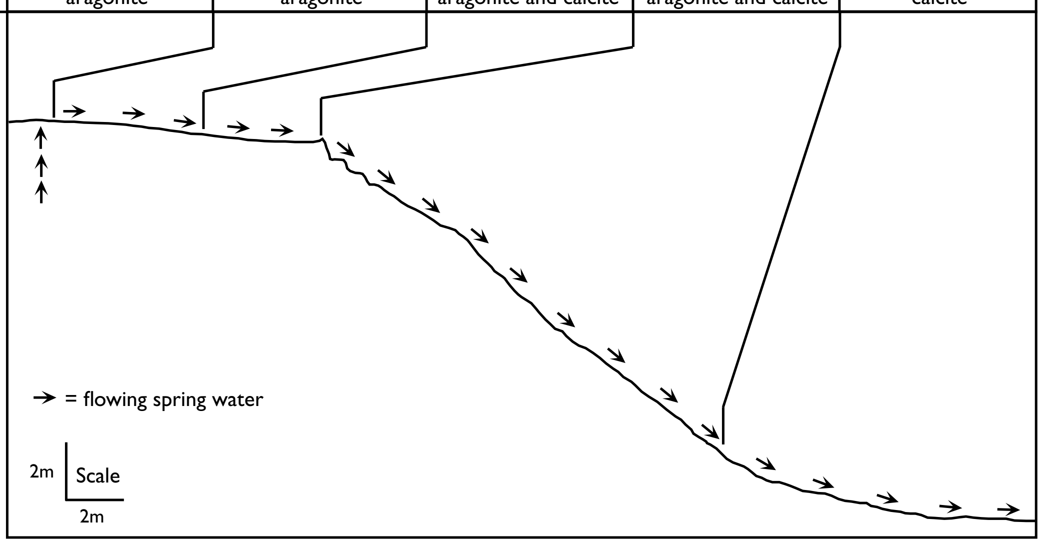


Figure 2. (A) Field photograph of Angel Terrace Spring AT-1 at Mammoth Hot Springs (modified from Fouke et al. 2000, 2003; Fouke in press). (B) Schematic cross-section of Spring AT-1 indicating the basic physical and chemical attributes of the travertine and spring water within each travertine depositional facies (modified from Fouke et al. 2000, 2003; Fouke in press).

by grouping the travertine into packages of mineral deposition along the main spring water flow path (fig. 2). Called "facies," these groupings of travertine are defined by specific rock characteristics (i.e., crystal size, shape, structure, porosity, and chemistry) that represent the sum total of the physical, chemical, and biological processes active in the hot spring environment (Fouke et al. 2000). The travertine facies model is manifested as distinct packages of $CaCO_3$ deposited along a primary flow path within any given hot spring system and has been consistently observed around the world (Veysey et al. 2008). This facies model includes five distinct groupings: the vent, apron and channel, pond, proximal slope, and distal slope (fig. 2). Students and teachers in the STaRRS partnership used this model to learn about the hot spring systems, develop questions, design and carry out experiments, and develop a deeper understanding of the system.

The STaRRS partnership

The curriculum development and educational tools chosen for this STSP partnership were based on four dimensions: (1) the existing *Expedition Yellowstone!* curriculum, (2) the systems being studied by the university research team, (3) the cognitive and social needs of the students, and (4) specific safety issues in regard to conducting research in an area with thermal features. For example, instead of using thermometers that required insertion into the spring water, the students used infrared thermometers to take surface temperatures a few meters from the water. Use of tools that can measure from a distance, while not as accurate as probes, enabled the students to monitor springs that might otherwise be unsafe due to very hot water and fragile deposits and to gather data without altering the travertine formations.

The equipment needed to measure the water temperature and pH, travertine shapes, and microbial mat colors and shapes is relatively inexpensive and easy to use by teachers and students at a broad range of scientific expertise and grade levels. Use of a limited collection of measurements and the travertine facies model allowed teachers in grades 4–8 and their students to develop a basic operational understanding of the system.

During the 2008–2009 school year, nine public and private 5th–8th grade school groups participated in three aspects of the STaRRS partnership: (1) they helped to collect photo point images; (2) they obtained specific temperature, pH, atmospheric, and hot spring flow data within a 50 centimeters x 50 centimeters (20 in x 20 in) transect at locations in two different hot spring systems; and (3) they developed testable scientific questions and then conducted experiments in the field to test their hypotheses. The students completed analysis and synthesis of their data and observations immediately after returning from the field. The on-site experience culminated in student presentations. Further analysis and more formal presentations were made later to a wide range of audiences in their home communities. The students investigated a broad array of topics, such as the effects of humidity and flow rate on water temperature, pH, and microbial communities. The resulting list of scientific questions generated by students was remarkably similar to the questions driving ongoing university-level research at Mammoth.

ANA HOUSEAL

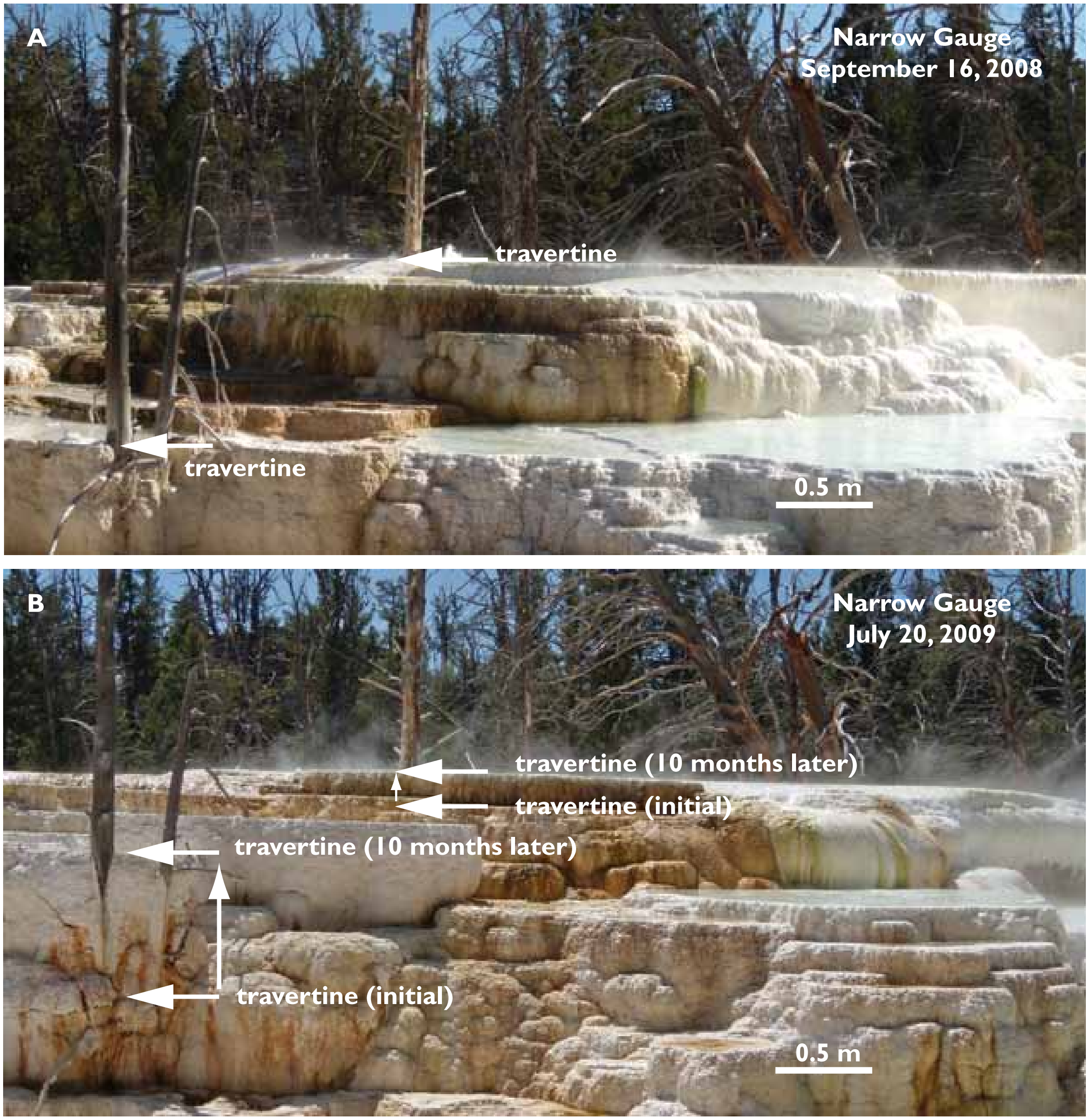
A STaRRS student checks the pH of Narrow Gauge Hot Spring.

The resulting list of scientific questions generated by students was remarkably similar to the questions driving ongoing university-level research at Mammoth.

Photo points

Photo points are designated locations where a standard digital camera (*Expedition Yellowstone!* STaRRS students used the Nikon P60) is used to capture a series of identically framed images over an extended period of time. These carefully selected sites have specific characteristics and importance for a given scientific field study. After months or years, the sequential images are combined into a time-lapse movie, providing invaluable information about springs, including simultaneous travertine and microbe growth dynamics.

The use of a long-term photographic record (photogrammetry) had been applied at Mammoth previously. A single location below the vent at Canary Spring in 2004 to 2006 was used in a recent study by the Illinois research group in collaboration with National Park Service rangers (Veysey and Goldenfeld 2008). Over a period of two years, 25 images were taken, aligned, and synthesized into a time-lapse movie that has been used in numerous educational and scientific forums and can be viewed at: http://guava.physics.uiuc.edu/projects/YNP/YNP_virtual_mammoth.html. However, logistics permitted only a limited number of images to be obtained over this two-year period. This resulted in irregular time gaps in recording the flow dynamics, microbial growth, and mineral deposition within the spring system. Optimally, this type of photographic record would include more frequent images taken over several years from several locations. This enhanced coverage could be augmented with photo point images and observations collected by STaRRS groups. The establishment of simple yet accurate protocols helps ensure that the images taken will be appropriate for scientific data collection.



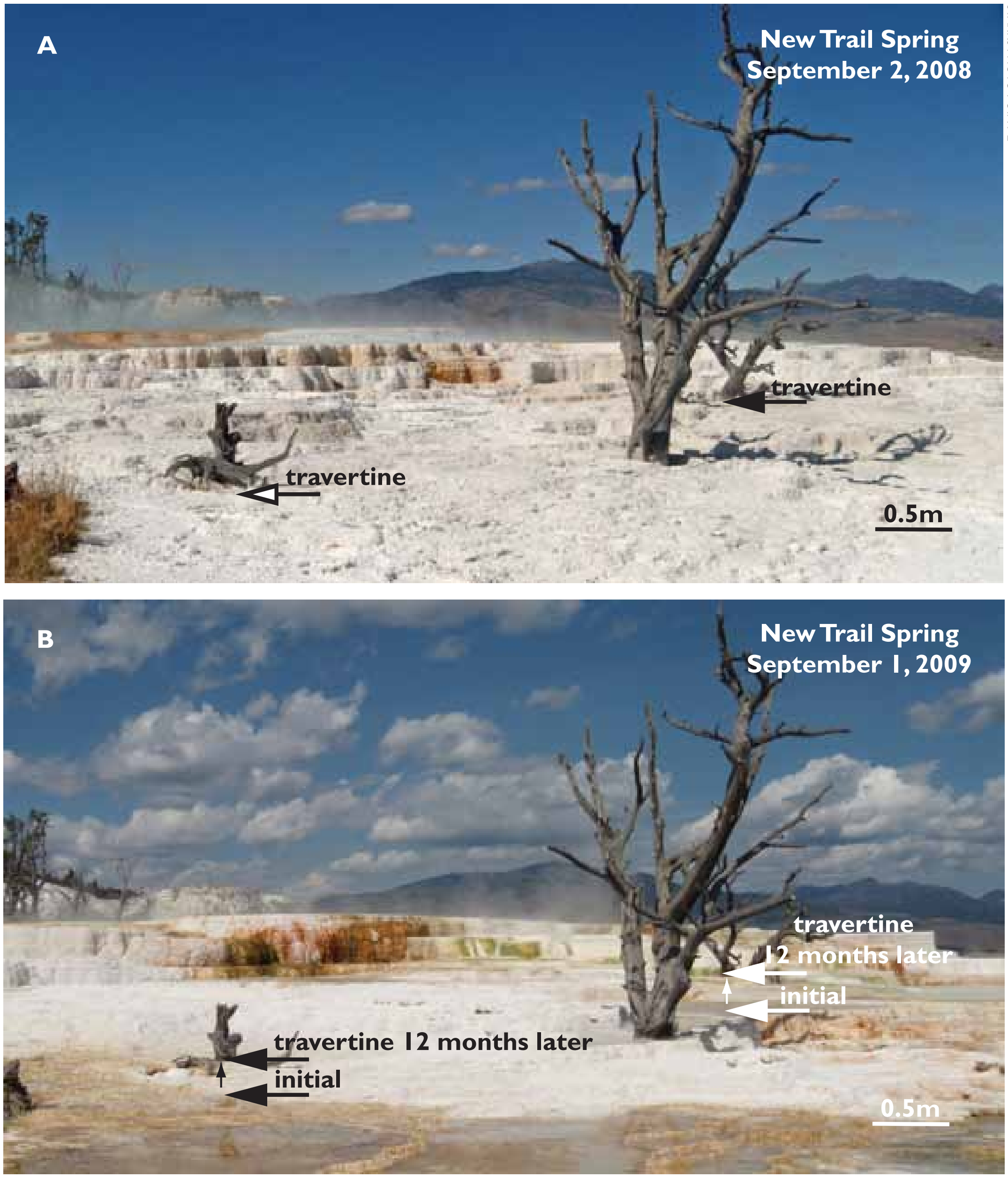
STARRS PHOTO POINT 7

Figure 3. Photo point field photographs taken at Narrow Gauge, Mammoth Hot Springs, (A) September 16, 2008, and (B) July 20, 2009. Note the remarkable 0.3–0.6 meters (approximately 1 to 2 feet) of travertine accumulation that took place over 10 months.

The STaRRS photo points

In July 2008, rangers and Ana Houseal set up eight photo point locations along the boardwalk at Canary Spring, Narrow Gauge Terrace, and Orange Spring Mound (fig. 1). In February 2009, when New Trail Spring (fig. 1) began to show signs of increased flow, two photo points were added along the boardwalk overlooking the spring. The photo point locations were selected so that (1) they were on a boardwalk or approved hiking trail for easy relocation and access, (2) the field of view contained an easily identified object to serve as a scale marker that could be used to align photos and measure changes, and (3) the camera brackets would not detract from visitors' view of the hot springs. The locations were also selected with the understanding that the springs are constantly changing, and some initially promising locations of strongly flowing spring water may not produce long-term results while slower flowing spots may end up becoming very active.

Of the eight photo point locations, the most striking example of the dynamic results provided by the photo point approach was the sequence taken at one of the three Narrow Gauge sites (fig. 3). Figures 3 and 4, which were created from photos collected by several different groups of STaRRS students and teachers, demonstrates how quickly travertine can accumulate. Over a 10-month period at Narrow Gauge, the thickness of the travertine increased from approximately 0.3 to 0.6 meters (1 feet to 2 feet; fig. 3).



STARRS PHOTO POINT 2

Figure 4. Photo point field photographs taken at New Trail Spring, Upper Terrace Boardwalk, Mammoth Hot Springs, (A) September 2, 2008, and (B) September 1, 2009. Note the travertine accumulation in the foreground and background, demonstrating the changes in flow direction and volume that took place over 12 months.

Benefits of the STaRRS partnership

The STaRRS partnership is now using the photo point image database before and after student expeditions to create interest, extend thinking, and deepen conceptual understanding related to the hot spring system. Having students gather images in the field and compare their images to those taken previously has helped reinforce understanding of the types and magnitude of the ecosystem processes active at Mammoth Hot Springs. Benefits for Yellowstone's Division of Interpretation include the use of photo point images for other school groups and ranger-led talks. Eventually, images may also be used in an interpretive display to help visitors understand the rapid changes occurring at Mammoth. The photo point images add to the growing collection of hot springs data, ready for use in the development and investigation of new hot-spring geobiology research.

Yet the true potential for student contributions to science using this model could be far greater, reaching beyond Mammoth and Yellowstone to other environments around the world. The STaRRS contribution has shown that time-series photographs captured by elementary students can be used to generate basic data useful to students and scientists. The tools and skills required to engage in this type of data collection (digital cameras, simple brackets, and computers) are readily available. Students and teachers are eager to find opportunities to engage in meaningful, real-world scientific research. The limiting factor need only be the imagination. The STaRRS model developed at Mammoth Hot Springs could easily be applied to other settings and provide insight on topics such as glacial retreat, post-fire plant succession, erosional processes, and even rising sea levels. This approach will also work in complex systems where change is constant but challenging to monitor. Schools and children are everywhere and elementary-aged students may be the world's most underutilized natural resource.

YS

Acknowledgements

This work was supported by a National Science Foundation (NSF) Biocomplexity in the Environment Program (EAR-0221743) grant award to Fouke and a supplementary NSF Research Experience for Teachers Program award. The conclusions of this study are those of the authors and do not necessarily reflect those of the funding or permitting agencies. We are greatly indebted to the input and support of many colleagues who made this study possible. We thank National Park Service rangers Brian Suderman, Trudy Patton, Melanie Condon, Michael Breis, Beth Taylor, Matt Ohlen, Sabrina Diaz, Christie Hendrix, and Henry Heasler for their tireless work to preserve Yellowstone resources while making them available for educational and scientific programs. We also thank the teachers and their school systems that participated in the STaRRS partnership. The intensive work and contributions of several members of the Fouke research group at the University of Illinois are also gratefully acknowledged, including the contributions of Amanda Oehlert, Holly Vescogni, Sam Dwyer, Mike Kandianis, Tom Schickel, and Roy Johnson.

ANA HOUSEAL

A STaRRS student checks the temperature in the distal slope near Orange Spring Mound.

TESA SIRONEN

Ana K. Houseal received her PhD in secondary and continuing education from the University of Illinois at Urbana-Champaign. The STaRRS partnership formed the basis for her dissertation research. She has been working with the education and interpretation staff at Yellowstone since 2006. **Bruce W. Fouke** is a Professor in Geology, Microbiology, and the Institute for Genomic Biology at the University of Illinois at Urbana-Champaign. His ongoing geomicrobiology research is to determine how the activity of specific living microbes or microbial communities influence the precipitation of common carbonate mineral deposits. **Robert Sanford,** PhD, is an environmental microbiologist and Research Associate Professor at the University of Illinois at Urbana-Champaign Department of Geology. **Robert Fuhrmann** has been Yellowstone's Education Program Manager in the Division of Interpretation since 1998. **Ellen Petrick** is a former education specialist at Yellowstone. She is currently the Education Specialist at Curecanti National Recreation Area and Black Canyon of the Gunnison National Park.

References

Allen, E.T., and A.L. Day. 1935. *Hot springs of the Yellowstone National Park*. Carnegie Institution of Washington. Publication No. 466, 525 p.

Bargar, K.E. 1978. Geology and thermal history of Mammoth Hot Springs, Yellowstone National Park, Wyoming. U.S. Geological Survey Bulletin 1444, 54 p.

Butler, S.K. 2007. *A facies-controlled model of Pleistocene travertine deposition and glaciation in the northern Yellowstone region*. University of Illinois Urbana-Champaign, Urbana, Illinois, 77 pp.

Fouke, B.W. (in press). Hot-spring systems geobiology: Abiotic and biotic influences on travertine formation at Mammoth Hot Springs, Yellowstone National Park, USA. *Sedimentology*.

Fouke, B.W., G.T. Bonheyo, E. Sanzenbacher, and J. Frias-Lopez. 2003. Partitioning of bacterial communities between travertine depositional facies at Mammoth Hot Springs, Yellowstone National Park, USA. *Canadian Journal of Earth Sciences* 40:1531–1548.

Fouke, B.W., J.D. Farmer, D.J. Des Marias, L. Pratt, N.C. Sturchio, P.C. Burns, M.K. Discipulo. 2000. Depositional facies and aqueous-solid geochemistry of travertine-depositing hot springs (Angel Terrace, Mammoth Hot Springs, Yellowstone National Park, U.S.A.). *Journal of Sedimentary Research* 70(3):565–585.

Kandianis, M.T., B.W. Fouke, R.W. Johnson, J. Vesey, W.P. Inskeep. 2008. Microbial biomass: A catalyst for $CaCO_3$ precipitation in advection-dominated transport regimes. *Geological Society of America Bulletin* 120(3/4):442–450.

Rye, R.O., and A.H. Truesdell. 2007. The question of recharge to the deep thermal reservoir underlying the geysers and hot springs of Yellowstone National Park. In *Integrated Geoscience Studies in the Greater Yellowstone Area: Volcanic, Tectonic, and Hydrothermal Processes in the Yellowstone Ecosystem*. L.A. Morgan, ed., 235–270. U.S. Geological Survey.

Sorey, M.L. 1991. *Effects of potential geothermal development in the Corwin Springs Known Geothermal Resources Area, Montana, on the thermal features of Yellowstone National Park*. Water Resources Investigation Report 91-4052. Menlo Park, CA: U.S. Geological Survey, 210 p.

Sturchio, N.C., K.L. Pierce, M.T. Murrell, and M.L. Sorey. 1994. Uranium series aging of travertine and timing of the last glaciation in the northern Yellowstone area, Wyoming-Montana. *Quaternary Research* 41:265–277.

Tinker, R.F. 1997. Student scientist partnerships: Shrewd maneuvers. *Journal of Science Education and Technology* 6:111–117.

Vescogni, H.S. 2009. *Microbial biomarkers: Mineralogy, crystal fabric and chemistry of calcium carbonate mineralization*. University of Illinois Urbana-Champaign, Urbana, Illinois, 64 pp.

Veysey, J., B.W. Fouke, M.T. Kandianis, T.J. Schickel, R.W. Johnson, and N. Goldenfeld. 2008. Reconstruction of water temperature, pH, and flux of ancient hot springs from travertine depositional facies. *Journal of Sedimentary Research* 78:69–76.

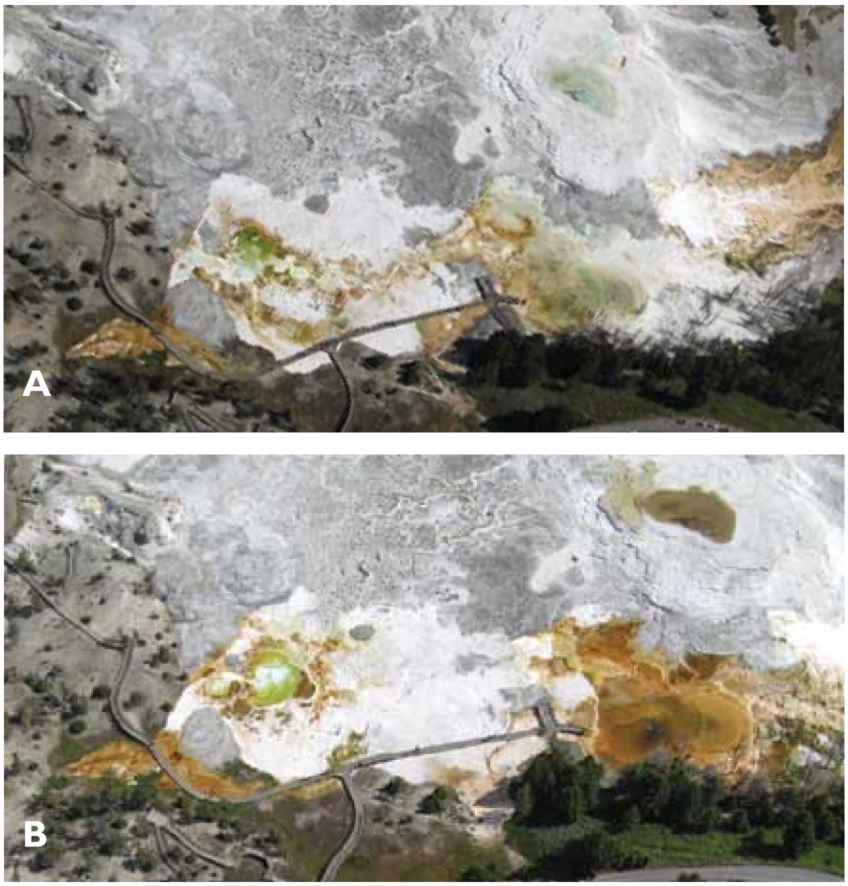
Veysey, J. and N. Goldenfeld. 2008. Watching rocks grow. *Nature Physics:* 4(4):1–4; 1–5.

White, D.E., R.O. Fournier, L.P.J. Muffler, A.H. Truesdell. 1975. *Physical results of research drilling in thermal areas of Yellowstone National Park, Wyoming.* Professional Paper 892. U.S. Geological Survey.

It's Not Drying Up, Just Changing

Mapping Change at Mammoth Hot Springs Using Aerial Photographs and Visual Observations

Brett B. Carr, Cheryl Jaworowski, and Henry P. Heasler



Helicopter oblique photographs of Canary, Main and Trail springs in August 2009 (A) showing new hydrothermal activity along the southern edge of the Main Terrace and (B) a similar area in July 2010. Notice that the vent locations are the same, but the boundaries of the flowing hydrothermal water and area covered by the colorful microbial mats have changed.

Early explorers, park personnel, and visitors have observed changes on the terraces of Mammoth Hot Springs for the past 130 years. Mammoth Hot Springs is a dynamic hydrothermal system where the presence of flowing thermal water at specific vents is seldom constant. Springs can form or dry up in a matter of days, switch between periods of activity and inactivity multiple times in a given year, or remain active for years in the same general location, dry up, and then reinitiate.

Since the first explorations of Yellowstone National Park, scientists have asked the same question about the fluctuations in water flow at Mammoth Hot Springs that many visitors ask today: "Are the springs drying up?" From 1928 to 1932, researchers Eugene Thomas Allen and Arthur Lewis Day studied the outflow of thermal water and documented a decline. Like park visitors, they wondered whether a prevailing drought had any effect upon the thermal water flowing on the Mammoth terraces. They summarized their investigation in 1935 saying: "It has been concluded by observers of the US Geological Survey, that spring water when it ceases to flow at any point in this area, as it not infrequently does, reappears in equal amount at some other point, so that the aggregate discharge remains constant." Studies by Bargar (1978) and Sorey (1991) argue for "continual change in the location and flow rate of individual vents."

Previous studies of Mammoth Hot Springs show that thermal water discharge can vary seasonally (Sorey 1991; Freidman and Norton 2007; Allen and Day 1935). The studies attribute the variability to the hydraulic pressure exerted on the hydrothermal systems by the volume of water entering the system at the surface. When the volume is high during the spring and early summer, greater pressure is exerted and more thermal water is discharged at the outlet of the system. The thermal water flowing on the terraces accounts for approximately 10% of the total discharge of the Mammoth hydrothermal system (Sorey 1991). Most of the remaining hydrothermal water discharges at Boiling River. Therefore, the thermal water discharge at Boiling River is one indicator of the total discharge of thermal water in the Mammoth hydrothermal system.

Despite the wealth of observations since 1871, when the Hayden survey described Mammoth Hot Springs, there are few maps showing the locations of flowing thermal water over time. Our goal was to create a series of maps or "snapshots in time" that show flowing hydrothermal water and the dynamic nature of the Mammoth hydrothermal system.

Study area

Located outside the 640,000-year-old Yellowstone caldera, Mammoth Hot Springs formed in the northern part of Yellowstone National Park, five miles south of Gardiner, Montana (fig. 1). The Mammoth hydrothermal system forms terraces composed of travertine (a sedimentary rock made of calcium carbonate) from the Upper Terrace Drive (Pinyon Terrace) to the Gardner River. The historic Fort Yellowstone, park headquarters, Mammoth Hotel, Mammoth campground, and other buildings in Mammoth Hot Springs were built on the travertine terraces.

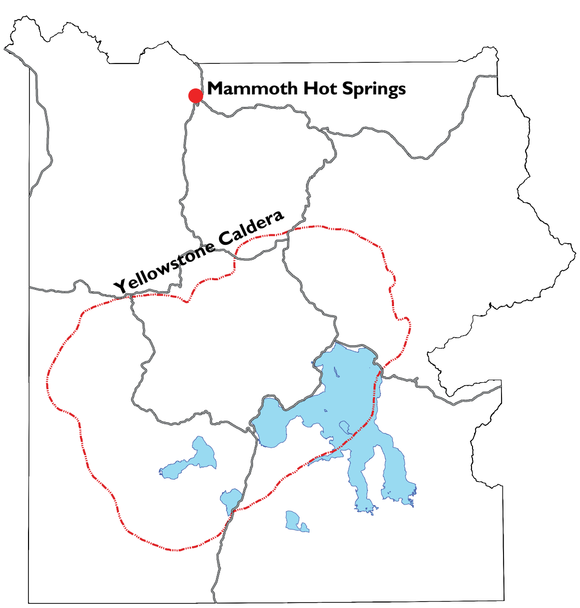


Figure 1. Map showing the location of Mammoth Hot Springs relative to the Yellowstone caldera.

Geology

Examination of Yellowstone's bedrock map helps place the Mammoth hydrothermal system in a parkwide, geologic context (USGS 1972). The Mammoth hydrothermal system is one of the few hydrothermal areas in Yellowstone National Park that has carbonate-rich hot spring deposits. Glacial sediments overlie travertine and the travertine overlies sedimentary and volcanic rocks. During the last 2.1 million years, the Yellowstone volcano has covered parts of the region with tuffs (a volcanic rock made of glass, pumice, and small rocks) and basaltic lava flows (Christiansen 2001). Fifty million years ago, the Absaroka volcanism affected the Mammoth area; today Sepulcher Mountain and Bunsen Peak are reminders of that volcanic past. Outcrops of sedimentary rocks, 550-million- to 100-million-year-old limestones, sandstones, siltstones, and shales are reminders of a geologic past dominated by shallow seas. The limestones are crucial to the formation of the Mammoth terraces as the rock supplies the carbonate necessary for building them.

The Norris–Mammoth corridor, a zone of faults trending generally north–south, stretches from the edge of the 640,000-year-old Yellowstone caldera to Mammoth Hot Springs (Pierce 1991). The faults in this region may allow groundwater near Norris to reach a depth where it is heated and provide a potential path for the heated water to reach Mammoth (Sorey 1991). The other potential source of the Mammoth hydrothermal water is localized deep circulation of water from the Gallatin Mountains interacting with a possible local heat source beneath Mammoth (Kharaka 1991).

Methods

Bargar's 1978 geologic map of Mammoth Hot Springs provided the basis for mapping areas covered by thermal water. In total, we created 11 maps showing flowing thermal water from 1954 to 2010 (table 1), including nine maps (1954–2006) generated from historical aerial photographs. For 2009 and 2010, we sketched visual observations of flowing thermal water on Bargar's geologic map and used air-oblique photography from 2009 and 2010 to confirm and edit the sketched field maps. We converted the mapped areas showing thermal water into polygons using ArcGIS software.

The three types of aerial photographs, black and white (B&W), color infrared (CIR), and true color, generated different quality maps (table 1). On a CIR aerial photograph (fig. 2), vegetation shows up as a bright red color. Healthy vegetation emits near-infrared radiation, which is not visible to the human eye. A true-color image shows the landscape as a human would see it. Some aerial photographs (1969, 1994, 2001, and 2006) were georectified. The process of georectification, or tying airborne images to known places on the ground, makes it easier to work with multiple

Table 1. Date, type, source, and method for obtaining the thermal water polygons and thermal water area for each of the nine aerial photographs and two field maps used in this study.

Year	Day	Type	Source	Polygon Method	Area (m^2)
1954	Sep 14	B&W	HRC	Scan and draw	8,500
1964	Sep 12	B&W	ETIC	Scan and draw	28,200
1969	Sep 7	Color	HRC	Feature extraction	30,300
1976	Sep 8	Color	ETIC	Scan and draw	21,800
1988	Oct 6	CIR	HRC	Scan and draw	31,500
1994	Sep 3	B&W	USDA	Feature extraction	15,800
1998	Aug 5	CIR	HRC	Scan and draw	17,900
2001	Aug 25	CIR	Sanborn	Feature extraction	14,300
2006	Aug 14	Color	NAIP	Feature extraction	20,000
2009	Aug 26	Field map	Authors	Map and draw	32,900
2010	Jun 21	Field map	Authors	Map and draw	21,400

aerial photographs in geographic information (ArcGIS) and image processing software (ENVI). The US Department of Agriculture Aerial Photo Field Office in Salt Lake City, Utah (www.apfo.usda.gov), has an aerial photography archive where many of the photographs used in this project are stored for public use.

Overexposure of the bright white travertine presents a challenge during image processing (fig. 2). The first step in making hydrothermal water areas more visible was to improve the image contrast and easily distinguish vegetation from the highly reflective travertine. Once the image contrast was improved, we applied ENVI's automated feature extraction wizard (ITT Visual Information Services 2008) to each of the aerial photographs. Feature extraction uses spatial, spectral, and textural characteristics of an image to define areas sharing similar characteristics. We were able to optimize parameters and consistently identify the areas of flowing thermal water on the terraces. These areas were imported into ArcGIS and visually grouped into a set of larger areas, thus representing the thermal water from different vents or sets of vents on the terraces. Finally, we calculated the total area with flowing thermal water for each photograph.

Five photographs used in this study were not georectified: two digital photos downloaded from the National Park Service (NPS) Technical Information Center (ETIC) in Denver and three hard copies from the Yellowstone Spatial Analysis Center and Heritage and Research Center (HRC) in Gardiner, Montana. To create digital files, we scanned the hard-copy photographs at 1,200 dots per inch. We used Adobe Photoshop to increase the contrast between areas of flowing thermal water and other areas, and the georeferencing tools in ArcGIS to roughly align each photograph to a 2006 orthorectified, National Agriculture Imagery program (NAIP) true-color image. Then we used the ArcGIS editor tools to manually draw polygons around the areas on the terraces covered by thermal water. Finally, we calculated the total area of the polygons for each photograph (table 1).

We also used historical observations by NPS North District interpretive rangers from 1871 to the present. These observations confirmed where thermal water was present in the aerial photographs. No thermal water polygons were drawn without supporting visual evidence from the aerial photographs. Historical observations were not used for years in which feature extraction could be used to create the polygons on the aerial photographs (1969, 1994, 2001, and 2006).

Figure 2. Color infrared aerial photograph of the Mammoth terraces, August, 25, 2001. Around the buildings, the grass appears bright red (top right). Overexposure makes accurate identification of flowing hydrothermal water on the terraces difficult.

Results

We created 11 maps showing flowing thermal water at the Mammoth Hot Springs terraces from 1954 to 2010 (figs. 3A–I). Only the regions covered by flowing thermal water on aerial photographs or visually observed are shown on the maps. Historical observations by NPS interpretive rangers (NPS 2009) may record activity, flowing thermal water, or inactivity where steam may be present.

Several general observations can be made about figures 3A–3I. The area near Palette Spring shows flowing thermal water on 9 of the maps and Canary Spring shows flowing thermal water on 10 of the maps. Considering the entire span of 56 years, most of Mound, Jupiter, and Palette terraces were active at some point between 1954 and 2010. Flowing thermal water from active springs is also present in the vicinity of the Upper Terrace Drive between 1954 and 2010, but difficult to map using aerial photographs.

Decadal variability

According to observations by North District interpretive rangers, thermal water flowed somewhere on Mound Terrace from 1904 through 1963 and has been inactive since 1989. Mound Terrace shows eastward flowing thermal water on the 1964, 1969, 1976, and 1988 aerial photographs (figs. 3B, C, and D) whereas the 1994, 1998, 2001, and 2006 aerial photographs (figs. 3E, F, and G) show no colorful, thermal water flowing east. Colorful hydrothermal water began flowing from the north side of Mound Terrace in November 2007 and continues at present. The 2009 and 2010 maps (figs. 3H and I), generated by visual mapping along the boardwalks, show this north-flowing hydrothermal water.

New Palette Spring shows flowing thermal water on the 1964, 1969 (fig. 3B), and 1976 (fig. 3C) aerial photographs, but none on the 1988 (fig. 3D) and 1994 (fig. 3E) aerial photographs, water is shown again on the 1998 aerial photographs. Visual mapping showed flowing thermal water during the summers of 2009 and 2010 (figs. 3H and I).

From 1954 until 1998, visitors and North District interpretive rangers observed flowing thermal water at Minerva Spring . The maps show Minerva Spring flowing in 1954 (fig. 3A), 1969 (fig. 3B), 1976 (fig. 3C), and 2001 (fig. 3F) and not flowing in 1964, 1988 (fig. 3D), and 1994 (fig. 3E). It is interesting to note that clear, hydrothermal water flowing on white and highly reflective travertine would not be visible or mapped on aerial photographs.

Hydrothermal springs along the Upper Terrace Drive are more dispersed and smaller than the thermal springs on the lower Mammoth terraces. Narrow Gage Spring, Orange Spring Mound, Highland Spring, and Angel Terrace show the most consistent hydrothermal activity over time.

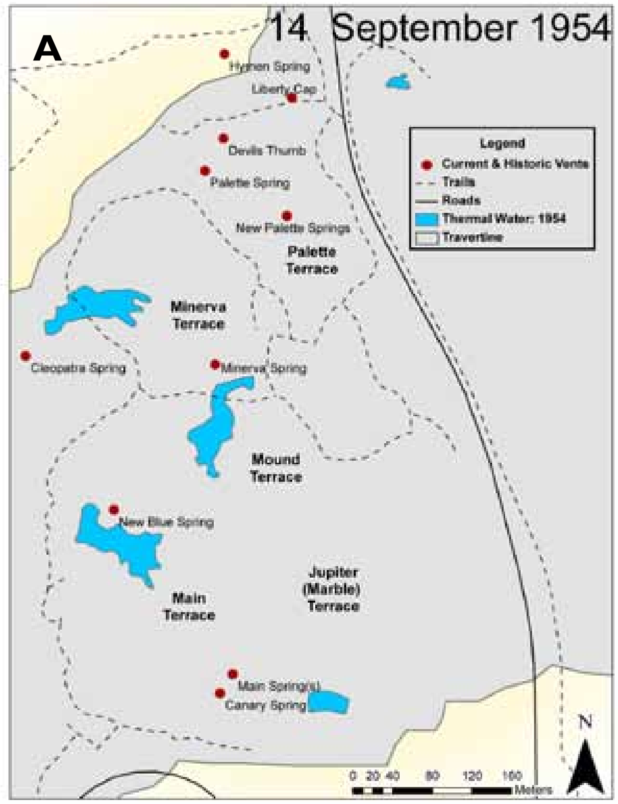
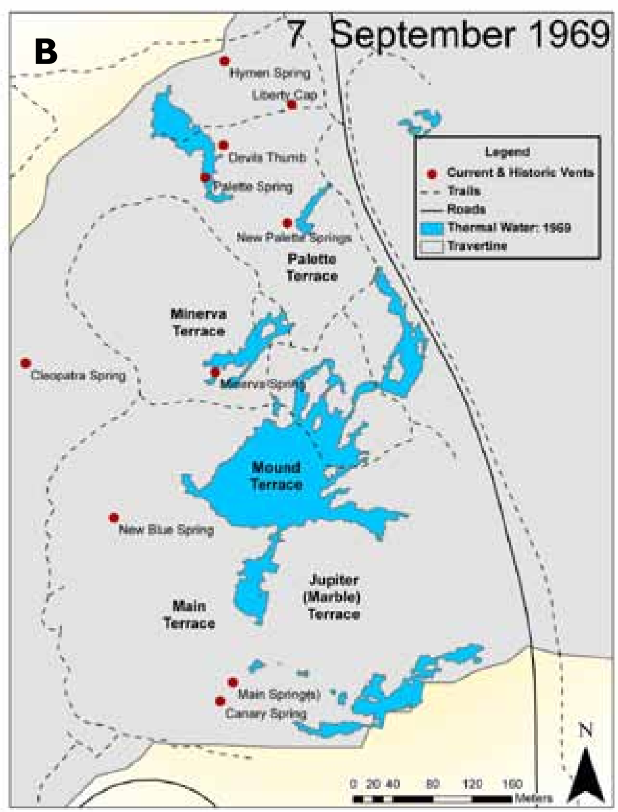
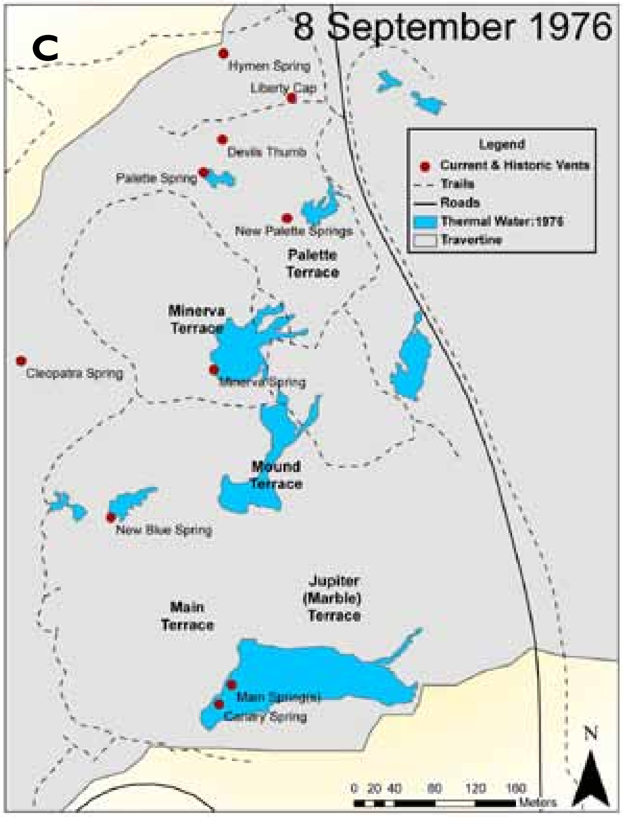
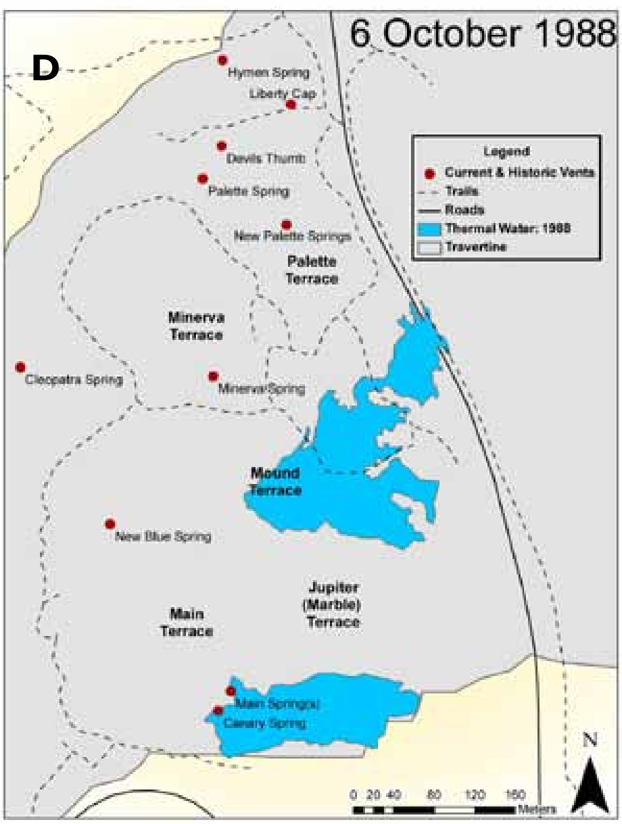
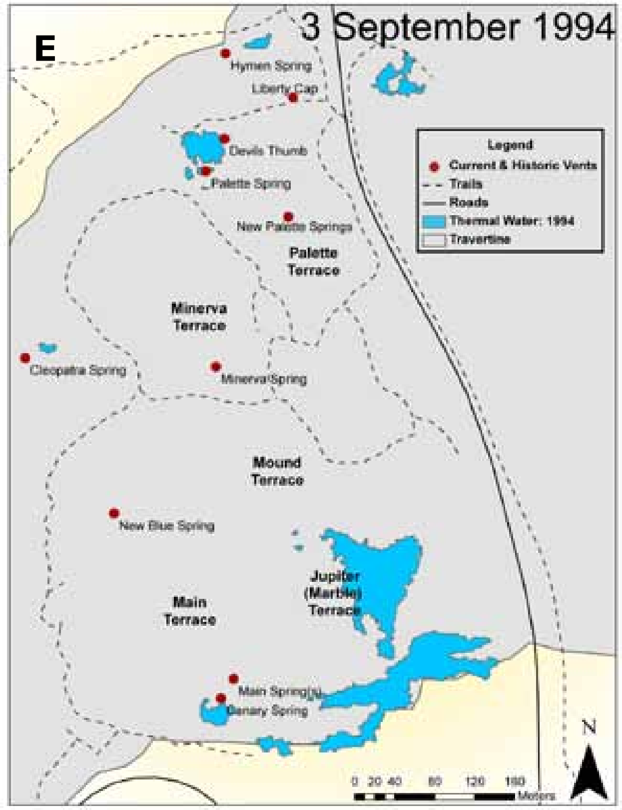


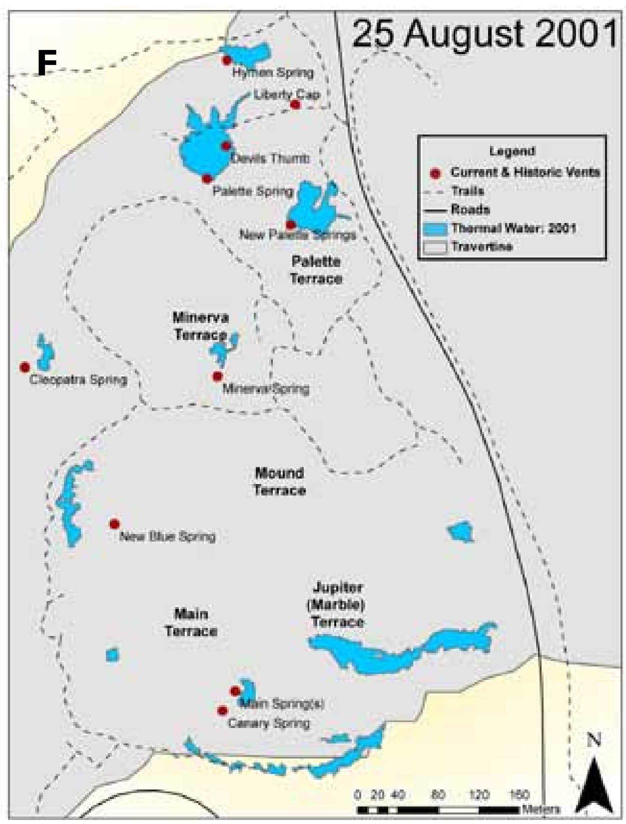
Figure 3 (A–I). Map of Mammoth Hot Springs showing the areas covered by hydrothermal water in (above in 1954). The gray area is the approximate boundary of the terraces based on observations of travertine, topography, and vegetation.




C
8 September 1976
Hymen Spring
Liberty Cap
Devils Thumb
Palette Spring
New Palette Springs
Palette Terrace
Minerva Terrace
Cleopatra Spring
Minerva Spring
Mound Terrace
New Blue Spring
Main Terrace
Jupiter (Marble) Terrace
Main Spring(s)
Canary Spring
Legend
Current & Historic Vents
Trails
Roads
Thermal Water:1976
Travertine
0 20 40 80 120 160
Meters
N


D
6 October 1988
Hymen Spring
Liberty Cap
Devils Thumb
Palette Spring
New Palette Springs
Palette Terrace
Minerva Terrace
Cleopatra Spring
Minerva Spring
Mound Terrace
New Blue Spring
Main Terrace
Jupiter (Marble) Terrace
Main Spring(s)
Canary Spring
Legend
Current & Historic Vents
Trails
Roads
Thermal Water: 1988
Travertine
0 20 40 80 120 160
Meters
N


E
3 September 1994
Hymen Spring
Liberty Cap
Devils Thumb
Palette Spring
New Palette Springs
Palette Terrace
Minerva Terrace
Cleopatra Spring
Minerva Spring
Mound Terrace
New Blue Spring
Main Terrace
Jupiter (Marble) Terrace
Main Spring(s)
Canary Spring
Legend
Current & Historic Vents
Trails
Roads
Thermal Water: 1994
Travertine
0 20 40 80 120 160
Meters
N

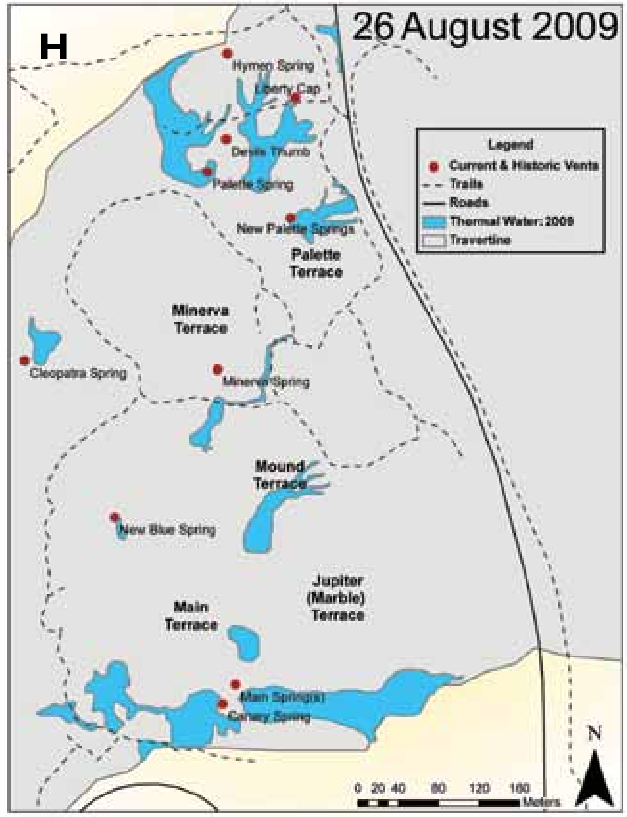

F
25 August 2001
Hymen Spring
Liberty Cap
Devils Thumb
Palette Spring
New Palette Springs
Palette Terrace
Minerva Terrace
Cleopatra Spring
Minerva Spring
Mound Terrace
New Blue Spring
Main Terrace
Jupiter (Marble) Terrace
Main Spring(s)
Canary Spring
Legend
Current & Historic Vents
Trails
Roads
Thermal Water: 2001
Travertine
0 20 40 80 120 160
Meters
N

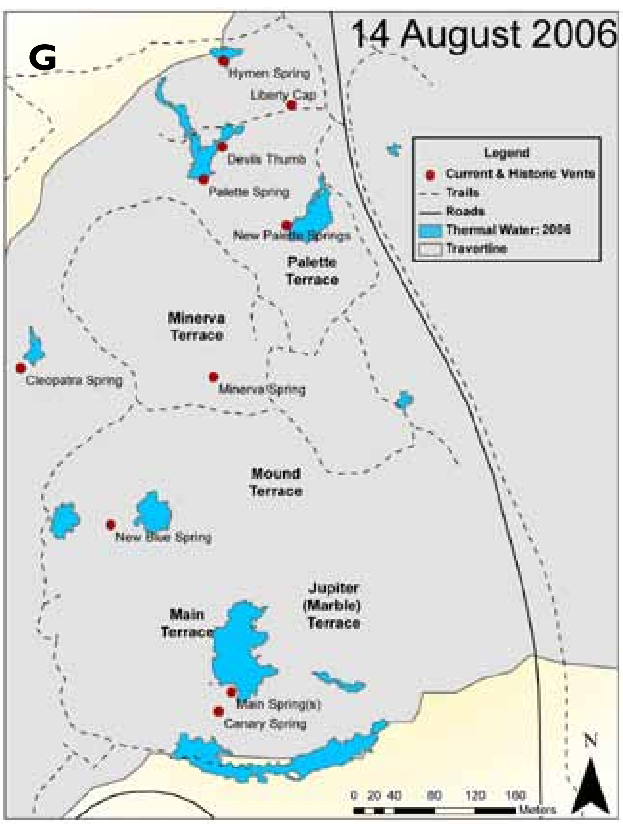
Annual variability

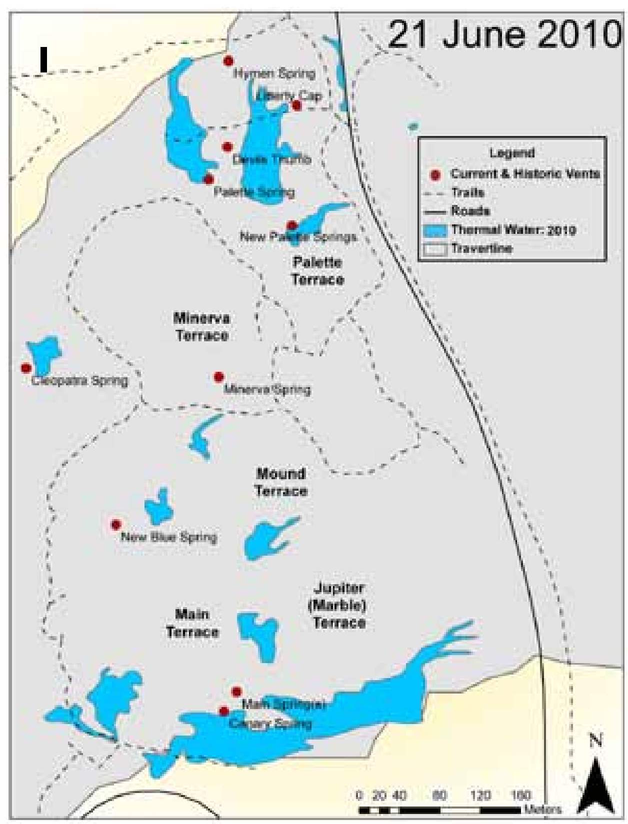
The 2009 and 2010 maps (figs. 3H and I) show the changes in flowing thermal water from year to year. The thermal activity at Canary, Palette, New Palette, and Jupiter springs seems relatively constant, but the thermal water flowing out of the vents varies in both direction and extent. Cleopatra Spring is the most similar between the two years, and Angel Terrace (not shown) was the most variable, with two new vents initiating in the past year.

Weekly and daily variability

Canary Spring provides an example of weekly variability in vents and the effect upon mapping flowing hydrothermal water. On the morning of September 11, 2006, Canary Spring stopped flowing thermal water. The following day, some thermal water began flowing from Canary's vent. During the next four days, flowing thermal water began to cover the colorful red-brown- and green-colored microbial mats. Aerial photographs and derived maps would show very different hydrothermal activity depending upon the day of the flight.







Discussion

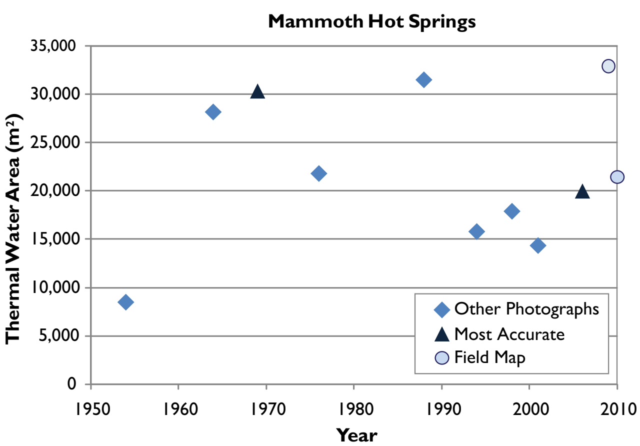
The various sources of aerial photographs (table 1) make consistency in the mapping of thermal water areas difficult. Areas with thermal water flow look very different on CIR, B&W, and true color aerial photographs. North District interpretive rangers observed flowing thermal water at Minerva Spring in 1964, 1988, and 1994. In contrast, our maps based on aerial photographs do not show flowing thermal water. On color aerial photographs, the presence of colorful microbial mats aids mapping of flowing thermal water and thermal pools. The area of flowing thermal water is easiest to pick out on the true-color, aerial photographs from 1969, 1976, and 2006, making them the most accurate maps. On the 2001 CIR aerial photograph, we identified an area appearing to be thermal water at Minerva Spring when the interpretive rangers reported no activity. However, when interpretive rangers use the term "no activity," steam and microbial activity may be present at a vent. The shades of gray in a B&W aerial photograph (1954, 1964, and 1994) make it difficult to distinguish between areas of flowing thermal water, shadows, or grasses on the terraces. Areas with clear or microbe-poor thermal water are almost indistinguishable from dry areas covered by young, white travertine. Further work is necessary to account for the discrepancies between human observations and the aerial photographs.

The ENVI feature extraction wizard provides a consistent application of parameters but does not eliminate bias in our maps. The extracted areas undergo subjective human analysis as contiguous areas of flowing thermal waters are mapped. Thus, human interpretation affects these estimates of flowing thermal water as the computer-generated areas are grouped visually.

The white-colored and highly reflective travertine terraces also affect the quality of the images. Most of the aerial photographs cover a wide area and include travertine, buildings, asphalt roads, and vegetation. This diverse landscape results in overexposure of the travertine terraces. For example, while North District Interpretation records indicate a large active area near Canary Spring in 2001, our 2001 map shows only a small area of flowing thermal water associated with the Canary Spring vent (fig. 3F). The overexposure on the 2001 CIR aerial photograph may underestimate the area covered by flowing thermal water at Canary Spring. In general, travertine terraces are less overexposed on the true-color images than the CIR or B&W images.

We place the most confidence on the area of flowing thermal water estimated for the 1969 (fig. 3B) and 2006 (fig. 3G) maps because both are true-color aerial photographs (green circles, fig. 4). Figure 4 shows the range of values from approximately 8,500 square meters to 33,000 square meters (91,300 ft^2 to 354,380 ft^2). It is interesting that our estimates of flowing thermal water for summer 2009 and 2010 (33,000 and 21,400 m^2) show a similar range of thermal water area (33,000 to 20,000 m^2) for 1969 and 2006. The 2009 and 2010 visual mapping from the boardwalks provides additional confidence in our area estimates derived from ENVI's automated feature extraction routine. For a visitor who saw the terraces in 1969 (figs. 3B and 4) and again in 1976 (figs. 3C and 4), it may appear that the terraces are drying up. In actuality, the visitor more likely witnessed the natural variability of flowing thermal water on the Mammoth terraces.

One assessment of the dynamic Mammoth hydrothermal system involves a comparison of the area covered by flowing thermal water (fig. 4) and the mean annual discharge of the nearby rivers. We know that the thermal water on the Mammoth terraces accounts for only 10% of the discharge from the Mammoth hydrothermal system (Sorey 1991) and that Boiling River is the primary source of thermal water discharge. Data collection began in 1989 for the Boiling River discharge (missing data from 1995 to 2002) and for the Gardner River in 1939 (missing from 1972 to 1984; see



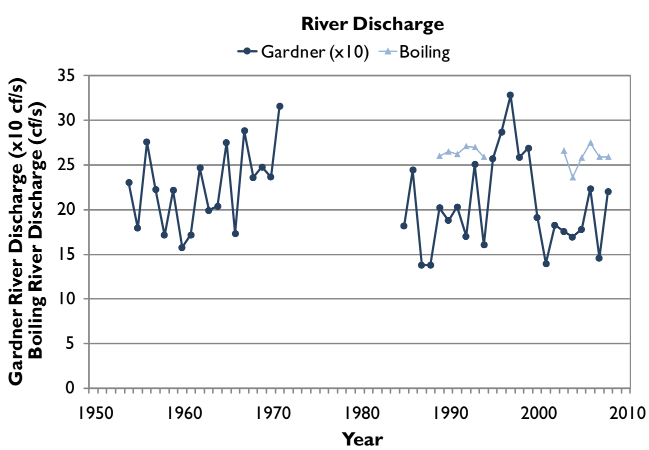


Figure 4. The thermal water area on the Mammoth terraces (top) is shown with the mean annual discharge for the Boiling and Gardner rivers (bottom). Discharge is displayed in cubic feet per second (cf/s). Thermal water area values are grouped in three ways: from field observations (circles), those believed to be the most accurate (triangles), and from historical aerial photos (diamonds).

We found no evidence to suggest that the volume of thermal water or level of activity changed significantly during the 56 years of visual record.

http://water.usgs.gov). Although data gaps make detection of trends difficult, there is no consistent increasing or decreasing trend in the total area covered by flowing thermal water on the Mammoth terraces. Nor is there any correlation between areas of flowing thermal water and the discharge of the Boiling or the Gardner rivers. Thus, the relatively constant discharge of Boiling River since 1987 (within 10% of the average) implies that there has been a relatively constant outflow of thermal water from the Mammoth hydrothermal system (fig. 4).

Summary

The maps in this article show the dynamic Mammoth hydrothermal system and the changes in flowing thermal water from year to year. Because thermal discharge can also change monthly, weekly, or daily, these maps do not capture all the variability of the system. Additionally, we produced initial estimates of the area covered by flowing thermal water on the Mammoth terraces. Comparison of the thermal water area to Boiling River discharge indicates a generally constant outflow of thermal water from the entire hydrothermal system. Changes in flowing thermal water on the terraces and errors in estimating the flowing thermal water cause variations in the area estimates. We found no evidence to suggest that the volume of thermal water or level of activity changed significantly during the 56 years of visual record. The appearance of the terraces, with their changing patterns of flowing thermal water, varies much more than the actual flow of water. We also applied a simple method for visually mapping the terraces that can be performed every year or multiple times a year. This mapping method can supplement aerial photography and easily document the changes at the Mammoth hydrothermal system.

YS

Acknowledgements

This project began in the summer of 2009 as part of the Geological Society of America's GeoCorps America Program. The geologists-in-the-park program is a collaborative partnership between the National Park Service Geologic Resources Division, the Yellowstone National Park geology program, and the Geological Society of America. During summer 2010, the Student Temporary Employment Program made it possible to continue this work. Brian Suderman, Supervisory Park Ranger with the Division of Interpretation, provided access to the historical observations by his interpretive staff, and Colleen Curry, Supervisory Museum Curator at the Heritage and Research Center, retrieved some aerial photographs. In addition, Brian Suderman and Jennifer Conrad, Supervisory Park Ranger with the Division of Interpretation, contributed information about ongoing changes at Mammoth Hot Springs. In 2009, Kevin Sattler, hydrologist at the USGS Montana Water Science Center kindly shared his hydrologic knowledge. My supervisors at the Yellowstone Center For Resources, Hank Heasler and Cheryl Jaworowski, provided guidance and support. I also thank my fellow 2009 GeoCorps participants, Chelsea Feeney and Tim Moloney, and 2010 GeoCorps participant Lindsey Harriman for helpful suggestions and ArcGIS expertise.

Brett B. Carr is a doctoral student at Arizona State University. He received a Bachelor of Arts degree in earth sciences from Dartmouth College in 2007 and a Master of Science degree in geophysics from University of Wisconsin in 2008.

Cheryl Jaworowski is a geologist at Yellowstone National Park. She received her doctorate in geology from the University of Wyoming and specializes in Quaternary geology and applying remote sensing to geologic mapping. **Hank Heasler** is the park geologist at Yellowstone National Park, specializing in geothermal systems.

References

Allen, E.T., and A.L. Day. 1935. Hot springs of the Yellowstone National Park. Carnegie Institution of Washington Publication 466, 525 p.

Bargar, K.E. 1978. Geology and thermal history of Mammoth Hot Springs, Yellowstone National Park, Wyoming. U.S. Geological Survey Bulletin 1444, 55 p.

Christiansen, R.L. 2001. The Quaternary and Pliocene Yellowstone Plateau Volcanic Field of Wyoming, Idaho, and Montana. U.S. Geological Survey Professional Paper 729-G.

Friedman, I. and D.R. Norton. 2007. Is Yellowstone losing its steam? Chloride flux out of Yellowstone National Park. In *Integrated Geoscience Studies in the Greater Yellowstone Area: Volcanic, Hydrothermal and Tectonic Processes in the Yellowstone Geoecosystem.* L.A. Morgan, ed., 275–297. U.S. Geological Survey Professional Paper 1717.

ITT Visual Information Services. 2008. ENVI Tutorial: Impervious Surface Feature Extraction, in ENVI 4.5 Fx Workshop.

Kharaka, Y.K., R.H. Mariner, T.D. Bullen, B.M. Kennedy, and N.C. Sturchio. 1991. Geochemical investigations of hydraulic connections between the Corwin Springs Known Geothermal Resources Area and adjacent parts of Yellowstone National Park. In *Effects of Potential Geothermal Development in the Corwin Springs Known Geothermal Resources Area, Montana, on the Thermal Features of Yellowstone National Park.* M.L. Sorey, ed. U.S. Geological Survey Water-Resources Investigations Report 91-4052, p. F1-F37.

National Park Service 2009. Hot Springs Records. Unpublished data.

Pierce, K.L., K.D. Adams, and N.C. Sturchio. 1991. Geologic setting of the Corwin Springs Known Geothermal Resources Area-Mammoth Hot Springs area in and adjacent to Yellowstone National Park. In *Effects of Potential Geothermal Development in the Corwin Springs Known Geothermal Resources Area, Montana, on the Thermal Features of Yellowstone National Park.* M.L. Sorey, ed. U.S. Geological Survey Water-Resources Investigations Report 91-4052, p C1-C37.

Sorey, M.L. 1991. Summary and conclusions. In *Effects of Potential Geothermal Development in the Corwin Springs Known Geothermal Resources Area, Montana, on the Thermal Features of Yellowstone National Park.* M.L. Sorey, ed. U.S. Geological Survey Water-Resources Investigations Report 91-4052, p A1-A17.

Yellowstone's Thermophiles

Microbial Diversity from Harsh Environments

Dennis W. Grogan

JASON HATCHER

Yellowstone National Park harbors a unique microbiota adapted to the chemical compositions and extremely high temperatures of its hydrothermal features. The extreme thermophiles that have been cultured from these environments span a tremendous range of evolutionary diversity, and the history of their analysis illustrates their value for basic research, biotechnology, and informed conservation. Rabbit Creek thermal area.

Extremely thermophilic microorganisms in Yellowstone National Park were first documented systematically by Thomas Brock and his students from about 1965 through 1971. They probed various hydrothermal environments using some simple but informative techniques, one of which involved immersing clean glass slides in hot springs and examining them microscopically after several days. The slides became coated with a film of diverse microbial cells and micro-colonies, showing that microorganisms in the hot spring were attaching to the surface and possibly reproducing there (Brock 1978). In another method, water samples from hot springs were supplemented with nutrients and incubated at temperatures typical of the original spring (65°C–85°C, or about 150°F–185°F). In several cases, dense populations of microorganisms developed, which were then re-cultured to yield pure cell lines (also called "clones," "strains," or "isolates"). Once a pure culture was established in the laboratory, it was relatively simple to test the effects of temperature, pH, and other culture conditions on the organism's rate of growth. The results confirmed that the microorganisms recovered from Yellowstone's hydrothermal environments did not simply survive the extremely high temperatures found in these environments, but required them.

One of these thermophiles (literally, "heat lovers") went on to become Yellowstone's most famous microbe. *Thermus aquaticus* was officially described in 1969 as a rod-shaped bacterium that requires oxygen and organic nutrients for growth, and grows best at a pH of about 7.7 and temperature of 70°C (Brock and Freeze 1969). As one of the most thermophilic organisms known at the time, *T. aquaticus* attracted attention from specialists interested in enzyme stability and other cellular adaptations to high temperature. In the mid-1980s, however, it was pushed onto center stage when its DNA polymerase became the key component in a technique for amplifying small intervals of DNA in a test tube. The new technique, called "polymerase chain reaction" (PCR), became valuable to molecular biologists and anyone else interested in detecting, analyzing, or recovering DNA sequences with great sensitivity. Patents issued to Cetus Corporation and later sold to Hoffman-LaRoche covered the thermostable polymerase and the PCR process (Gelfand et al. 1989), and the popularity of the technique generated huge profits.

Although the material critical to this invention was a microorganism discovered in a national park by academic researchers, neither the US government nor the researchers were entitled to royalty-free use of the technology or a share of the income. The legal situation prompted the National Park Service (NPS) and Yellowstone National Park to draft a policy for "benefits sharing" to govern microbiological and related research. The policy, which was recently approved by the director of the NPS, requires researchers to negotiate a cooperative research and development agreement (CRADA) with the NPS before commercializing technology derived from materials collected in the park. The draft policy survived a major legal challenge in April 2000 when a US federal court ruled that a CRADA did not, in itself, compromise the NPS mission of preservation and conservation. The ruling is also consistent with the fact that most CRADA bioprospecting involves removing only small environmental samples, followed by culturing or molecular cloning in laboratories off-site. Ironically, the patent on the *T. aquaticus* DNA polymerase, which had initially motivated the policy, failed a legal challenge of its own. In December 1999, a US District Court ruled the patent invalid, based on evidence that the DNA polymerase cited in the patent application was the same one documented years earlier by researchers at the University of Cincinnati (Chien et al. 1976).

Given this species' dramatic history, complete with colorful personalities, revolutionary technology, massive profits, legal intrigue, and a Nobel Prize, one can understand why many take *T. aquaticus* as the icon of Yellowstone's "extremophiles." From a microbiologist's perspective, however, it seems important to stress that this species is not the only extreme thermophile living in Yellowstone, the most thermophilic, or even the most interesting, but is simply one of the first to be coaxed into reproducing in captivity. The succession of thermophiles that has followed it, and the molecular signatures of many more that remain uncultured, point to the largely unappreciated complexity of Earth's geothermal microbiota and the value of exploring it in biological terms.

Metabolic diversity

Although *T. aquaticus* requires extremely high temperatures for growth, the basic outlines of its metabolism are familiar. Each *Thermus* cell takes up dissolved organic compounds from its liquid environment and breaks them down into somewhat simpler molecules, collectively called intermediary metabolites. The growing *Thermus* cell assimilates some of this material, but oxidizes the rest of it to water and CO_2 in order to generate energy. Many microorganisms, as well as the mitochondria of eukaryotic cells, follow this strategy of consuming organic compounds supplied by the environment and are classified as "heterotrophs," signifying that they "feed" on "something else."

However, many of Yellowstone's thermophiles discovered after *T. aquaticus* have been found to live by radically different strategies. A number of them, for example, produce their cellular material from CO_2, as the chloroplasts of green plants do, and are thus classified as "autotrophs" (literally, "self-feeders"). In doing this, however, these thermophiles do not use the Calvin-Benson-Bassham pathway of CO_2 fixation found in chloroplasts. Furthermore, they obtain the energy required to drive the process not by absorbing sunlight, but by oxidizing and reducing various chemicals provided by the geochemistry of their environment. *Acidicaldus* spp. for example, use oxygen to oxidize elemental sulfur to sulfuric acid; part of the resulting electrons are channeled through oxidative phosphorylation to generate ATP and the rest are transferred to CO_2 to generate intermediary metabolites and new cellular material. Other Yellowstone thermophiles find alternative electron acceptors in their hydrothermal environments to substitute for oxygen. *Thermoterrabacterium ferrireducens* and *Geothermobacterium ferrireducens*, for example,

JASON HATCHER

A small bubbling mudpot, Central plateau.

Measuring the temperature of a small hydrothermal outflow on the central plateau.

use ferric ions (Fe^{+3}) as the oxidizing agent. Another interesting oxidation-reduction process, whose metabolic significance remains less clear, is the oxidation of arsenite to arsenate by other bacteria in some Yellowstone hot springs (D'Imperio et al. 2007). If arsenic metabolism sounds unhealthy, one must consider that a bacterium isolated from the Norris Geyser Basin, *Thermosinus carboxydivorans*, derives both cell carbon and energy from carbon monoxide (Solokova et al. 2004). This thermophile therefore challenges the classical distinction between heterotroph and autotroph, and has perhaps the chemically simplest diet of any known organism. These various metabolic strategies sound complex and bizarre, but they share a practical logic, because they enable the organism to harvest some form of energy provided by the geochemistry of its hydrothermal environment.

Furthermore, these apparently unusual thermophiles are familiar in terms of the structure and compositions of their cells, because they share many basic features of other bacteria, including the *Escherichia coli* cells diagramed in biology textbooks, the *Yersinia pestis* that caused the bubonic plague of medieval Europe, and the soil Actinomycetes that produce various antibiotics. All these microorganisms consist of cells about one micrometer in diameter that lack a true nucleus or any other membrane-enclosed organelles. In these cells, the cytoplasm is contained within a phospholipid bilayer, which is surrounded and supported by a cell wall composed of peptidoglycan, a cross-linked polymer found only in bacterial cells. Some bacteria, designated Gram-negative because of certain staining properties, have a second, outer membrane just outside the cell wall that incorporates another uniquely bacterial substance, lipopolysaccharide (figs. 1A and 1B).

Evolutionary diversity

Although bacteria are common in extreme environments, many of the microorganisms found in geohydrothermal environments differ fundamentally from bacteria as well as from the larger, more complex eukaryotic cells of protozoa, fungi, plants, and animals. These Archaea, which Carl Woese first described as a third form of life, are evolutionarily distinct from both bacteria and Eucarya (eukaryotes) (Woese et al. 1990). Woese's discovery was based originally on analyses of the ribosomal RNA sequences found in all cells (fig. 2), but differences can be seen in cell structure as well (fig. 1).

Archaeal cells resemble bacterial cells with respect to their small size and lack of nuclei and other internal organelles. However, they have neither peptidoglycan cell walls nor phospholipid in their cytoplasmic membranes (CM). Outside the CM, most archaea have only a protein layer, formed by a highly ordered array of subunits that are anchored to the underlying membrane and interact strongly with each other (fig. 1C). The archaeal CM also differs from its bacterial counterpart, being composed of unique lipids in which long isoprenoid chains (hydrocarbons built up from 5-carbon isoprene units), rather than fatty acids, are linked to glycerol via ether linkages rather than ester linkages. In addition to these properties not found in bacteria, archaea have various proteins closely related to those of eukaryotic cells. These molecular similarities are consistent with analyses of highly conserved gene families that indicate archaea share a non-bacterial ancestor with modern eukaryotes (Woese et al. 1990).

The first archaea from Yellowstone National Park were isolated several years before this distinct lineage of cellular life was recognized. By about 1970, Brock's group had succeeded in culturing microorganisms from some of the strongly acidic hot springs and pools found in Yellowstone and other thermal regions of the world. The cells were small, with a round, irregularly creased shape which Brock's group described as lobate. Brock's group cultured several isolates of this type, all of which grew optimally in acidic medium (about pH 3) at a temperature of about 80°C (175°F). The isolates differed somewhat with respect to other growth properties, however, and although most have since been lost, it seems likely that they would now be considered different *Sulfolobus* species. For example, two of the surviving strains were both cultured from a pool called Locomotive Spring in the Norris Geyser basin: 98/3 is the type strain of *Sulfolobus acidocaldarius* (Brock et al. 1972), whereas 98/2 appears to represent the rather different species *Sulfolobus solfataricus* (Rolfsmeier and Blum 1995).

The defining characteristics of this new genus were novel and unexpected, and they generated both fascination and skepticism among scientists. Although bacteria that oxidized sulfur and required acidic environments were known at the time, such bacteria were rod-shaped and could not tolerate high temperature. *Sulfolobus* cells revealed, in addition to their lobate shape, an unusual, flexible layer of glycoprotein subunits as an apparent substitute for a peptidoglycan cell wall (figs. 1C and 1D). Having described these striking cellular features, Brock and his coworkers went on to focus on *Sulfolobus* ecology. They made their cultures available to other researchers, however, and other groups isolated new *Sulfolobus* strains from similar geohydrothermal environments around the world.

A world of hyperthermophilic archaea

The availability of *Sulfolobus* cultures prompted various laboratory studies on their cellular and biochemical properties. The results revealed similarities between *Sulfolobus* and some fundamentally different but equally unusual microorganisms, including the extreme halophiles (which require extremely high salt concentrations for growth) and the extremely oxygen-sensitive methanogens (which derive energy from certain substances by converting them into methane).

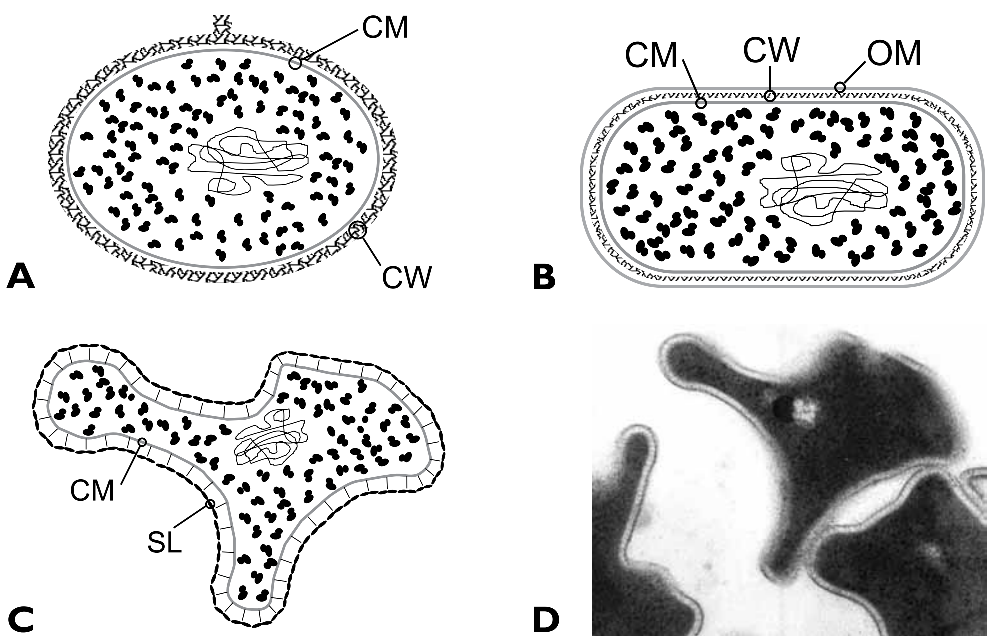


Figure 1. Distinct cellular architectures of Bacteria and Archaea.

The upper panels illustrate the two most common cell types of bacteria (Gram-positive [A] and Gram-negative [B]). Both types have DNA concentrated inside the cell, but not enclosed in a nucleus. A cytoplasmic membrane (CM) encloses the DNA, ribosomes, and other components of the cytoplasm. Panel A shows a typical Gram-positive cell, where the CM is enclosed by a thick cell wall (CW). Panel B shows a typical Gram-negative cell, which has a thinner CW and an additional, exterior membrane, called the outer membrane (OM). All bacterial cell walls are composed of peptidoglycan, and all bacterial membranes contain phospholipid.

The two lower panels depict cells of Archaea. Panel C is a schematic diagram showing compacted DNA and a CM reinforced structurally from the outside, analogous to bacterial cells. However, in Archaea the CM consists of isoprenoid ether lipids and is reinforced by a flexible, proteinaceous S-layer (SL). The CM lipids contain C_{20} and C_{40} isoprenoid chains ether-linked to sn2,3 glycerol phosphate, and the SL consists of glycoproteins subunits that associate to form a flexible, two-dimensional lattice around the cell. Panel D shows a transmission electron micrograph (thin section) of *S. acidocaldarius* cells in which the basic features illustrated in the diagram (Panel C) can be seen.

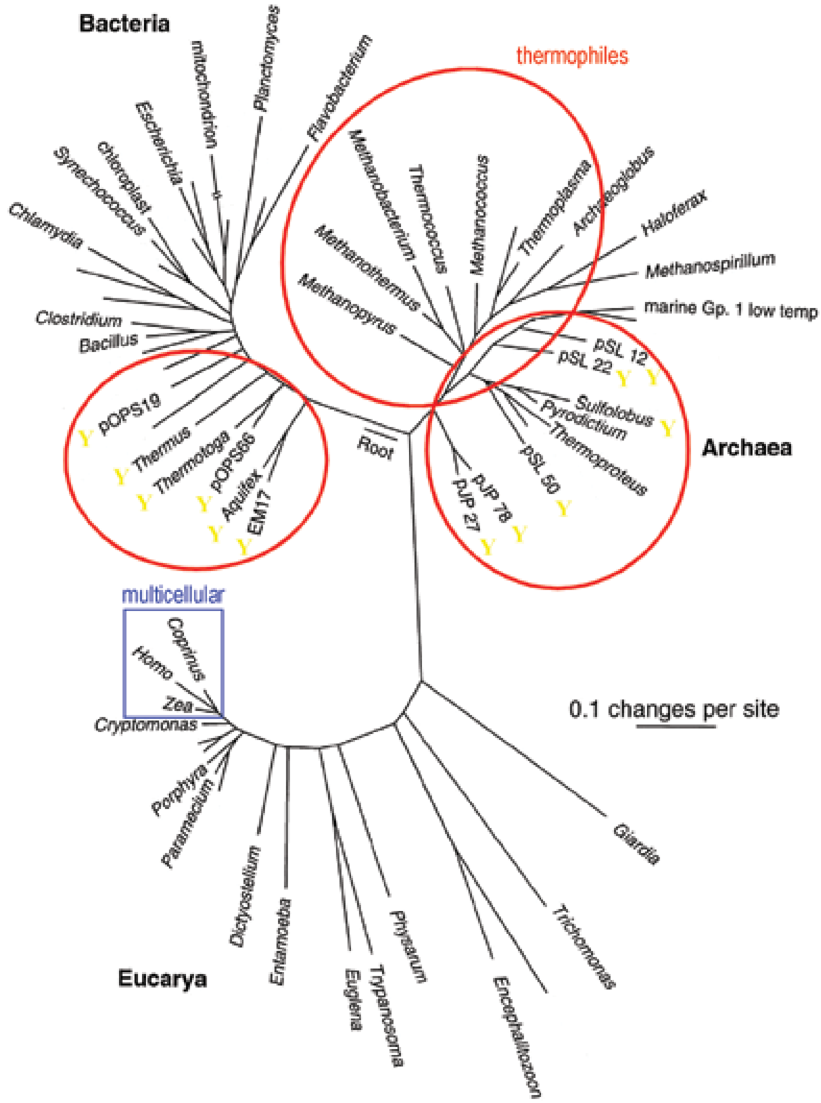


Figure 2. The Tree of Life from a molecular perspective.

This dendrogram, adapted from Pace (1997), shows the evolutionary relatedness of small-subunit ribosomal RNAs (ssu-rRNAs) from representative genera of cellular organisms. This RNA is one of the few gene products that occurs in all cells and carries out the same function, thus allowing divergence of its sequence to be measured between any two organisms. This divergence is represented on the dendrogram by the combined length of the two branches joining any two organisms. These evolutionary distances reveal several significant patterns:

The cryptic diversity of single-celled organisms. Species of plants, animals, and fungi are defined by visible morphological differences, but single-celled organisms appear very similar by this criterion; this results in severe under-estimation of microbial diversity. When the molecular divergence of all cellular organisms is compared on a common basis, the diversity of single-celled organisms dwarfs that of multicellular plants, animals, and fungi (blue box).

The relatedness of Archaea and Eucarya. Additional analyses (not described here) place the root of the ssu-rRNA tree along the base of the bacterial branch, as indicated in the figure. This means that the first major evolutionary split gave rise to the bacterial lineage, on one hand, and an ancestor shared between Archaea and Eucarya, on the other. This shared ancestor is consistent with many molecular features besides the ssu-rRNA sequences that archaea and eukaryotes share but do not appear in bacteria.

Thermophilia as a primitive characteristic. Branches leading to thermophilic organisms emerge from near the base of their respective groups, which are marked by the red circles. This may indicate that early bacterial and archaeal cells may have also been adapted to extremely high temperatures.

The diversity of Yellowstone thermophiles. Organisms cultured or detected in hydrothermal systems within Yellowstone National Park have been marked by an orange letter Y on the dendrogram. Some of the branches are identified by clone number, not genus name. These represent ssu-rRNA sequences cloned from thermal environments, and indicate the extensive diversity of extreme thermophiles that have not been cultured.

The properties shared by these otherwise divergent groups of microorganisms provided additional evidence supporting Carl Woese's three-domain phylogeny. In turn, Woese's identification of the evolutionary distinctiveness of Archaea intensified interest in the molecular features of archaea from extreme environments. Teams of microbiologists, including several European groups, applied new isolation strategies to geohydrothermal environments and succeeded in cultivating a series of new thermophiles.

Unlike *Sulfolobus* spp., many of the new thermophiles were anaerobic, and several defined new metabolic strategies. For example, the thermophilic, rod-shaped anaerobes *Thermoproteus* and *Pyrobaculum* were found to reduce sulfur to hydrogen sulfide. Members of a third group, *Acidianus*, had a *Sulfolbus*-like cell shape, but were shown to switch between oxidative and reductive modes of sulfur metabolism depending on the availability of oxygen. Archaea were later discovered that can oxidize ferrous iron in solution or as insoluble metal sulfides, or precipitate realgar, an arsenic sulfide, as an end-product of metabolism (Huber et al. 2000). The oxidation of metal sulfides also has a practical application, as it increases the recovery of copper and other metals from sulfidic ores, and this continues to be developed for the mining of low-grade ores (Nemati et al. 2000). The archaeal successors to *Sulfolobus* also set new temperature records. *Pyrodictium occultum*, isolated from shallow marine events near Vulcano, Italy, grows optimally at about 103°C, for example, whereas the current record-holder in culture, *Pyrolobus fumarii*, grows optimally at 106°C, can still grow at 113°C, and can survive brief periods of autoclaving (121°C) (Blöchl et al. 1997).

Into the laboratory

Consistent with their record-breaking growth temperatures, the anaerobic hyperthermophiles have various unusual cellular features that raise questions about the early evolution of cellular life and how biological processes can be sustained at such high temperatures. Unfortunately, however, these organisms remain difficult to culture, and experimenting on them often requires Herculean effort and skill. In contrast, the relatively simple culturing conditions and vigorous growth of *Sulfolobus* species enables non-microbiologists to produce their own cell mass, which facilitates detailed study of *Sulfolobus* enzymes and other cellular features. As a result, throughout the 1980s and 1990s, *Sulfolobus*, especially *S. solfataricus* strains isolated from Italy, became increasingly popular subjects for biochemistry and molecular biology. This trend intensified with the sequencing of the *S. solfataricus* and *S. tokodaii* genomes in the late 1990s.

During this period, few labs focused on Brock's Yellowstone isolates, but those that did were rewarded with interesting phenomena. At the University of Nebraska, Paul Blum's group investigated carbohydrate metabolism in Yellowstone isolate 98/2, purifying several carbohydrate-degrading enzymes (Rolfsmeier and Blum 1995) and isolating mutant strains in which some of these enzymes had been inactivated or their expression altered. Later studies investigated the regulation of gene expression and mechanisms of heavy metal resistance (Dixit et al. 2004). Meanwhile, the author began studying *S. acidocaldarius* (isolate 98/3), whose vigorous growth seemed promising for genetic manipulation, and discovered in it a form of conjugation in which cells pair and transfer pieces of DNA. The transferred DNA can recombine into the corresponding site of the recipient chromosome, and can thus displace any mutation at that location (Grogan 1996). Based on the resilience of the process under laboratory conditions, it is expected to occur in natural *Sulfolobus* populations, and to affect their genetic diversification over time.

The author's students at the University of Cincinnati went on to investigate the process of mutation in specific *S. acidocaldarius* genes. This revealed that *Sulfolobus* replicates its DNA with an accuracy matching that of *E. coli*, despite the fact that the pH and temperature within the *Sulfolobus* cell predict a 1000-fold faster rate of spontaneous DNA damage (Jacobs and Grogan 1997). This observation and others suggest that *Sulfolobus* cells repair their DNA very efficiently. Most details of the repair strategies remain mysterious, however, because genes related to several DNA repair genes of other organisms do not occur in the genome of any *Sulfolobus* species or any other hyperthermophilic archaeon (Grogan 2004). However, one repair strategy, photo-reversal of UV damage, has been demonstrated biologically (Grogan 1997), and the gene encoding the necessary enzyme has been identified genetically. The likelihood that additional DNA repair systems operate in these archaea and use novel mechanisms, remains an important research question.

Back to nature

Genetic analyses of microorganisms require reliable "plating," a basic microbiological technique that rarely succeeds for hyperthermophilic archaea (Huber et al. 2000). Plating involves solidifying liquid growth medium to form a sterile gel, usually in a petri dish, and then spreading or streaking a few cells on the surface of the gel. When the resulting plate is incubated under suitable conditions, an isolated microbial cell on the plate surface grows and divides for many generations, producing a visible mound (colony) representing up to several million identical daughter cells. The technique can be used in a preparative sense, to generate pure cultures, or in a quantitative sense, to count the number of viable cells in a suspension.

Adapting this technique to *Sulfolobus* required solving several technical problems. For example, the traditional gelling agent, agar, melts near the incubation temperatures needed for *Sulfolobus* and decomposes in strong acid. Thus, a substitute had to be found which could withstand the combination of high temperature, low pH, and long incubation times required for *Sulfolobus* colonies to form. Fortunately for *Sulfolobus* research, a commercially available gelling agent, gellan gum, works admirably and requires only minor modifications to traditional plate-pouring procedures. Another incubation problem, rapid drying of the plates, can be solved by sealing them inside plastic bags or other containers for incubation.

Through the 1990s, as *Sulfolobus* plating became increasingly reliable, the author was struck by two trends in the scientific literature. First, new *Sulfolobus* species were being described at a fairly steady pace, but none originated from Yellowstone despite the fact that this region has probably the largest network of acidic thermal features in the world. Second, all *Sulfolobus* species, new and old, had been isolated by the classical technique of liquid enrichment, despite publication of the fairly straightforward *Sulfolobus* plating procedure (Grogan 1989). Because liquid enrichment generally yields only the fastest-growing species from a complex mixture of microorganisms, it remained unclear whether the environments that yielded the existing *Sulfolobus* species also contained species that were missed simply because they were being out-competed during liquid enrichment.

The situation raised the following question: What would emerge if someone isolated extreme thermoacidophiles from locations throughout Yellowstone National Park by plating samples directly, with no liquid enrichment? The presumed answer was that much greater diversity would be recovered. The idea was integrated with a summer laboratory course and the author's ongoing genetic research in a proposal to the National Science Foundation, which was eventually funded.


JASON HATCHER

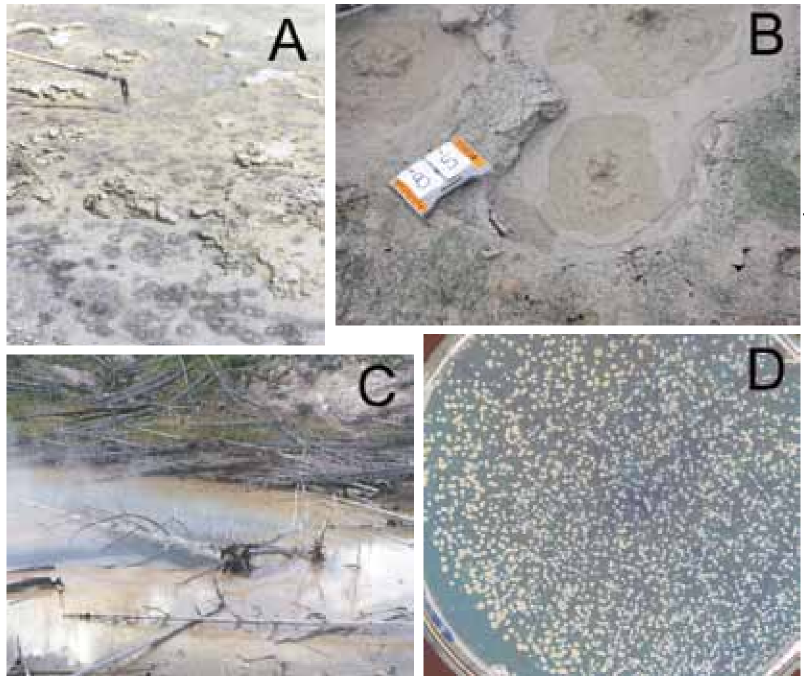
Mudpots often outnumber the available sampling vials. Photo at Turbid Lake.

Sampling *Sulfolobus* populations in Yellowstone

The *Sulfolobus* culturing scheme that has emerged from this NSF-sponsored project involves six stages: (1) selecting suitable thermal sites in the park, (2) measuring temperature and pH in the hydrothermal features, (3) taking fluid and sediment samples back to the laboratory, (4) plating on acidic medium, (5) evaluating the diversity of colonies that form, and (6) purifying and cryo-preserving a subset of these strains. Site selection relies heavily on advice and help provided by staff of the Yellowstone Center for Resources (YCR) and park volunteers. In particular, the Spatial Analysis Center has compiled an inventory of thermal features that can be searched online through the Research Coordination Network website (http://www.rcn.montana.edu/), which provides a valuable resource for researchers interested in getting a permit to sample thermal features of particular types or in particular locations. In addition, YCR staff advise researchers, approve the sites, and relay current conditions at many thermal areas, helping ensure that the work is done safely and out of public view. Although public visibility or hazardous conditions eliminates a number of interesting areas, it has become clear that the remaining *Sulfolobus* habitat will, at the current pace, require decades to sample.

Figure 3 shows some acidic thermal pools that were selected for sampling. At each site, the temperatures of pools and springs are measured by a pole-mounted thermometer (fig. 3A) to identify those between about 65 and 85°C. These waters are then tested to identify those that have pH between about 2.5 and 4.5. From these springs, about 10 milliliters (0.3 fl. oz.) of water plus solid material (sand, gravel, or silt) are scooped into a sterile glass vial, also mounted on a long pole. Airspaces are left in the vials, and the samples are stored and transported at ambient temperature. Alternative strategies such as excluding air or adding a buffer to moderate the pH have been tested on replicate samples, but did not increase the yield of viable cells significantly. Within five days, the samples are taken back to the laboratory, where small volumes of both diluted and undiluted samples are spread on gellan gum plates containing acidic nutrient medium. Plates are incubated at 76 to 78°C and examined for colonies after seven to eight days. Of the 15–20 samples typically taken from a given thermal area, about half usually yield colonies, and in a few of these, the numbers can be extremely high (fig. 3D).

Many microbial ecologists discourage the culturing of microorganisms as a means of analyzing natural microbial



PANELS A AND C: BRIAN KINKLE; B: JASON HATCHER; D: DENNIS GROGAN

Figure 3. Cultivating *Sulfolobus* from Yellowstone National Park. Panels A–C: Acidic thermal pools sampled for *Sulfolobus* isolates. Dead trees indicate that relatively recent shifts in subsurface conduits have caused acidic fluids and steam to emerge in a formerly wooded site. Panel D: Photograph of a plate demonstrating a high concentration of viable cells. A hot spring sample was diluted by a factor of 20 with sterile acidic buffer, and about 0.2 milliliters of the resulting dilution were spread over the surface of a gellan gum plate and incubated at 76°C–78°C for more than one week. The *Sulfolobus* colonies on this plate number about a thousand, and vary in diameter and other visible properties.

communities because, as a rule, this yields only a small fraction of the species and viable cells present, and thus presents an inaccurate picture. Culturing nevertheless has one important advantage over purely molecular analyses, which is that each strain recovered can be grown indefinitely and therefore analyzed to great resolution. The direct-plating technique standardized in the author's laboratory also provides quantitative (if rather rough) comparisons of the abundance of culturable *Sulfolobus* cells in acidic thermal features throughout Yellowstone National Park.

The direct-plating data collected so far depict a highly patchy distribution of these culturable cells among hydrothermal features. For example, one thermal area has yielded colonies from every sample taken, while others with dozens of acidic pools and springs over thousands of square meters have yielded none. Most acidic thermal areas fall between these extremes, and the individual samples taken from them vary widely in culturable cell abundance. Taken together, the results suggest patchy population clusters with complex boundaries. The number of culturable cells generally does not correlate with temperature or pH values (within the acceptable range sampled), but other geochemical parameters of the samples have not been tested.

In addition to widely varying concentrations of culturable cells, the samples vary in the apparent diversity of the cells. When a sample yields a number of colonies on a plate, the colonies often differ with respect to size, color, and opacity, which argues for some biological differences among the clones (fig. 3D). However, as the Yellowstone isolates have been analyzed in molecular terms, it has become clear that this apparent diversity does not represent multiple species. Each *Sulfolobus* strain from Yellowstone that has been isolated in the author's lab by direct plating and subjected to DNA sequencing analysis has been found to be in one species with all the other Yellowstone isolates so analyzed, as well as with *Sulfolobus* strains isolated from Lassen Volcanic National Park, the Kamchatka peninsula of eastern Siberia, and Iceland. *Sulfolobus* isolates from Icelandic thermal areas had been informally named "*Sulfolobus islandicus*" by Wolfram Zillig's research group in Germany (Zillig et al. 1994), and some researchers have applied this name to all the closely related isolates from various world regions.

The plating conditions themselves do not seem to explain the consistent recovery of this single species from throughout the northern hemisphere, as several other *Sulfolobus* species grow well under the same conditions. Furthermore, hot spring samples from New Zealand plated under these same conditions in the same laboratory yielded colonies of a species very different from *S. islandicus* and closely related to *Sulfurisphaera*. Although the cultivation data remain incomplete, they suggest that *Sulfolobus* habitats in the northern hemisphere may be dominated numerically by *S. islandicus*, whereas other thermoacidophiles appear to dominate in some other world regions. It must be stressed that this numerical abundance does not preclude the possibility that other *Sulfolobus* species, such as *S. acidocaldarius* or yet-unknown species, persist at low levels in Yellowstone or elsewhere.

Levels of genetic diversity

Although the author's ongoing survey of Yellowstone has not yielded the diverse new species originally sought, it has preserved intraspecific diversity, which provides an interesting perspective on the genetics of *Sulfolobus* populations within the park. This diversity was first documented by collaborators

Yellowstone National Park supports large populations of diverse bacteria and archaea adapted to the extreme environmental conditions found only in hydrothermal systems.

using the technique of multilocus sequence typing (MLST), in which several genes important for basic cellular function, so-called "housekeeping genes," are sequenced from each isolate. The resulting DNA sequences are joined to form a composite genotype that can be compared across a number of isolates. MLST of *Sulfolobus* isolates from different thermal regions of the northern hemisphere put them into a common species, but generated discrete clusters which corresponded to the different regions sampled (Whitaker et al. 2003). Although such genetic endemism, a sign of allopatric speciation, is routinely observed with plant or animal populations, it is generally disputed for unicellular organisms, due to the efficiency of their passive dispersal.

In another study, multiple clones were cultured from two neighboring outflows of a thermal area in Kamchatka which approximate a single point on the relevant spatial scale. MLST of 60 isolates defined 17 distinct genotypes, demonstrating extensive genetic diversity within this limited sample of the local population. Statistical analyses of the alleles at the different MLST loci further indicated that most of this genetic diversity could be attributed to recombination among pre-existing genetic differences, rather than formation of new mutations (Whitaker et al. 2005). Such a combinatorial mode of genetic variation is known from both theoretical and experimental studies to provide a more efficient route to adaptive evolution than *de novo* mutation.

The genes chosen for MLST perform important cellular functions and, as a result, generally accumulate only relatively inconsequential substitutions of one DNA base for another, and do so at a slow rate. Sequencing of entire bacterial and archaeal genomes, however, shows a very different mode of variation on the genome-wide scale, namely the apparently random acquisition and loss of large DNA segments that often cover several genes. The faster pace and more drastic nature of these mutations compared to those measured by MLST raises the question as to whether variation of gene content among *Sulfolobus* genomes would reveal geographical patterning like that revealed by MLST. Hybridization of genomic DNA to microarrays of *S. solfataricus* probes was used to score the presence or absence of genes in eight *Sulfolobus* isolates recovered from four regions of the northern hemisphere. The analysis revealed many differences and, with one apparent exception, their pattern followed a geographical structuring similar to that seen previously in MLST (Grogan et al. 2008). Geographical pattern in these very different forms of genetic divergence reinforces the idea that *Sulfolobus* populations remain relatively isolated within the small islands defined by their hydrothermal habitat.

A third level of genetic variation in *Sulfolobus* is harder to quantify, and involves various entities collectively called mobile genetic elements. They are largely parasitic DNA sequences that occur in all cellular microorganisms and fall into three broad classes: transposable genetic elements, plasmids, and viruses. *Sulfolobus* strains from Yellowstone and other regions have been found to differ with respect to the genetic elements that actively transpose in their genomes (Blount and Grogan 2005). Similarly, a number of relatively large *Sulfolobus* plasmids have been found that can transfer themselves between strains (Greve et al. 2004). They are not known to confer any specific biological property on their host, however. As a result, these plasmids are normally detected through DNA analysis. One conjugative plasmid, for example, was discovered only when the DNA of its *Sulfolobus* host, a strain isolated from the Mud Volcano area, was sequenced.

The viruses of *Sulfolobus* and related archaea span a range of genome sizes and exhibit diverse and unusual characteristics. In several cases, classifying them has required the creation of entirely new families having no counterparts among bacterial, plant, or animal viruses (Prangishvili and Garrett 2004). *Sulfolobus* viruses may provide valuable tools for focused, mechanistic studies of molecular processes of hyperthermophilic archaea, which have proven difficult so far. In addition, since viruses function as predators to control the abundance of their host species in microbial communities, the study of *Sulfolobus* viruses should shed new light on the ecology of natural populations. The nature of the selective pressure that viruses exert on host populations, and the defenses that the hosts employ, represent compelling questions for current and future research.

In summary, Yellowstone National Park supports large populations of diverse bacteria and archaea adapted to the extreme environmental conditions found only in hydrothermal systems. They differ radically from historically familiar microorganisms, and represent a dynamic and largely under-appreciated natural resource. The gene sequences, thermostable enzymes, and basic knowledge gained from these thermophiles address scientific interests ranging from ecology to cellular physiology, and cellular evolution to biotechnology. Reliable cultivation methods allow *Sulfolobus* clones and populations to be studied in great detail, and the observations made so far raise new questions. Why, for example, are culturable *Sulfolobus* cells distributed so unevenly within geothermal features of apparently uniform characteristics? How severely do *Sulfolobus* populations fluctuate over time, and what factors dictate these dynamics? Do thermophilic bacteria adapted to hydrothermal habitats show geographical patterning of genetic diversity, as *Sulfolobus* populations do? The productive, and still relatively brief, history of culturing Yellowstone's thermophiles illustrates the value of basic research conducted in the park, and its fundamental compatibility with the preservation and conservation missions of the National Park Service.

YS

Acknowledgements

Many individuals have contributed to the author's research in Yellowstone over the past 10 years. Special thanks go to Christie Hendrix, Stacey Gunther, Liz Cleveland, and other YCR staff at park headquarters, and to field escorts Smokey Sturtevant, Ann Deutch, Carrie Guiles, Blake Weidenheft, and George Rice. Brian Kinkle, Norio Kurosawa, Jason Hatcher, Jack Young, Clyde Stauffer, and the author's family provided valuable field assistance. Members of the Grogan lab at the University of Cincinnati helped isolate, analyze, and preserve *Sulfolobus* cultures from Yellowstone sources; these include Katie Schmidt Sorg, Rebecca Perkins, Shannon Strini, Greg Dikos, Greg Bell, Josh Hansen, Zachary Blount, Cynthia Sakofsky, Michael Wolfe, and Dominic Mao, and the University of Cincinnati undergraduate students enrolled in the course "Micro-organisms from Extreme Environments." Additional thanks go to Ann Deutch, Christie Hendrix, and Brian Kinkle for comments on the manuscript. Culturing surveys conducted from 1999 through 2004 were funded by NSF grant MCB 9733303.

JASON HATCHER

Dennis Grogan grew up near Kansas City, Missouri; he majored in Biological Sciences and Chemistry at the University of Missouri–Columbia, where his involvement in undergraduate research intensified his interest in prokaryotic forms of life. He completed MS and PhD degrees in microbiology at the University of Illinois, Urbana–Champaign, with a focus on bacterial genetics and lipid metabolism. During graduate school, he became intrigued by the archaebacteria (as they were called then) through the research of Ralph Wolfe, Carl Woese, and others at the University of Illinois. This led to post-doctoral studies in the research groups of Wolfram Zillig (Max-Planck-Institute for Biochemistry), Giuseppe Bertani (NASA Jet Propulsion Lab), and Rob Gunsalus (University of California, Los Angeles). He is currently a professor in the Department of Biological Sciences at the University of Cincinnati, where he and his students analyze the genetic processes of *Sulfolobus* species.

References

Blöchl, E., R. Rachel, S. Burggraf, D. Hafenbrandl, H.W, Jannasch, and K.O. Stetter. 1997. *Pyrolobus fumarii*, gen. and sp. nov., represents a novel group of archaea, extending the upper temperature limit for life to 113 degrees C. *Extremophiles* 1:14–21.

Blount, Z.D., and D.W. Grogan. 2005. New insertion sequences of *Sulfolobus*: Functional properties and implications for genome evolution in hyperthermophilic archaea. *Molecular Microbiology* 55:312–325.

Brock, T.D. 1978. Thermophilic microorganisms and life at high temperatures. New York: Springer-Verlag.

Brock, T.D., K.M. Brock, R.T. Belly, and R.L. Weiss. 1972. *Sulfolobus*: A new genus of sulfur-oxidizing bacteria living at low pH and high temperature. *Archives of Microbiology* 84(1):54–68.

Brock, T.D., and H. Freeze. 1969. *Thermus aquaticus* gen. n. and sp. n., a nonsporulating extreme thermophile. *Journal of Bacteriology* 98(1):289–297.

Chien, A., D.B. Edgar, and J.M. Trela. 1976. Deoxyribonucleic acid polymerase from the extreme thermophile *Thermus aquaticus*. *Journal of Bacteriology* 127(3):1550–7.

D'Imperio, S., C.R. Lehr, M. Breary, and T.R. McDermott. 2007. Autecology of an arsenite chemolithotroph: Sulfide constraints on function and distribution in a geothermal spring. *Applied and Environmental Microbiology* 73(21):7067–7074.

Dixit, V., E. Bini, M. Drozda, and P. Blum. 2004. Mercury inactivates transcription and the generalized transcription factor TFB in the archaeon *Sulfolobus solfataricus*. *Antimicrobial Agents and Chemotherapy* 48(6):1993–9.

Gelfand, D.H., S. Stoffel, F.C. Lawyer, and R.K. Saiki. 1989. Purified Thermostable Enzyme, United States patent number 4,889,818, December 26, 1989.

Greve, B., S. Jensen, K. Brügger, W. Zillig, and R.A. Garrett. 2004. Genomic comparison of archaeal conjugative plasmids from *Sulfolobus*. *Archaea* 1(4):231–239.

Grogan, D.W. 1989. Phenotypic characterization of the archaebacterial genus *Sulfolobus*: comparison of five wild-type strains. *Journal of Bacteriology* 171(12):6710–9.

———. 1996. Exchange of genetic markers at extremely high temperatures in the archaeon *Sulfolobus acidocaldarius*. *Journal of Bacteriology* 178(11):3207–3211.

———. 1997. Photoreactivation in an archaeon from geothermal environments. *Microbiology* 143:1071–6.

———. 2004. Stability and repair of DNA in hyperthermophilic Archaea. *Current Issues in Molecular Biology* 6:137–44.

Grogan, D.W., M.A. Ozarzak, and R. Bernander. 2008. Variation in gene content among geographically diverse *Sulfolobus* isolates. *Environmental Microbio*logy 10(1):137–146.

Huber, R., H. Huber, and K.O. Stetter. 2000. Towards the ecology of hyperthermophiles: Biotopes, new isolation strategies and novel metabolic properties. *FEMS Microbiology Reviews* 24(5):615–623.

Jacobs, K.L., and D.W. Grogan. 1997. Rates of spontaneous mutation in an archaeon from geothermal environments. *Journal of Bacteriol*ogy 179(10):3298–3303.

Nemati, M., J. Lowenadler, and S.T. Harrison. 2000. Particle size effects in bioleaching of pyrite by acidophilic thermophile *Sulfolobus metallicus* (*BC*). *Applied Microbiolology and Biotechnolology* 53(2):173–179.

Pace, N.R. 1997. A molecular view of microbial diversity and the biosphere. *Science* 276(5313):734–740.

Prangishvili, D. and R.A.Garrett. 2004. Exceptionally diverse morphotypes and genomes of crenarchaeal hyperthermophilic viruses. *Biochemical Society Transactions* 32(2):204–208.

Rolfsmeier, M., and P. Blum. 1995. Purification and characterization of a maltase from the extremely thermophilic crenarchaeote *Sulfolobus solfataricus*. *Journal of Bacteriology* 177(1):482–5.

Sokolova, T.G., J.M. González, N.A. Kostrikina, N.A. Chernyh, T.V. Slepova, E. A. Bonch-Osmolovskaya, and F.T. Robb. 2004. *Thermosinus carboxydivorans* gen. nov., sp. nov., a new anaerobic, thermophilic, carbon-monoxide-oxidizing, hydrogenogenic bacterium from a hot pool of Yellowstone National Park. *International Journal of Systematic and Evolutionary Microbiology* 54:2353–9.

Whitaker, R.J., D.W. Grogan, and J.W. Taylor. 2003. Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science* 301(5635):976–8.

Whitaker, R.J., D.W. Grogan, and J.W. Taylor. 2005. Recombination shapes the natural population structure of the hyperthermophilic archaeon *Sulfolobus islandicus*. *Molecular Biology and Evolution* 22(12):2354–2361.

Woese, C.R., O. Kandler, and M. Wheelis. 1990. Towards a natural system of organisms: Proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences of the United States of America* 87:4576–9.

Zillig, W., A. Kletzin, C. Schleper, and I. Holz. 1994. Screening for Sulfolobales, their plasmids and their viruses in Icelandic solfataras. *Systematic and Applied Microbiology* 16(4):609–628.

From the Archives

NPS HISTORIC PHOTOGRAPH COLLECTION/-00225 AND F.1674. PHOTOGRAPHER: CRIBBS.

Professor Harvey of the University of Minnesota and Park Naturalist Frank Thore create moving pictures of algae in order to study plant life of the thermal waters at Mammoth Hot Springs, Yellowstone National Park, c. 1923.

The printing of *Yellowstone Science* is made possible through a generous annual grant from the nonprofit Yellowstone Association, which supports education and research in the park. Learn more about science in Yellowstone through courses offered by the Yellowstone Association Institute and books available by visiting www.yellowstoneassociation.org.

The production of *Yellowstone Science* is made possible, in part, by a generous grant to the Yellowstone Park Foundation from Canon U.S.A., Inc., through *Eyes on Yellowstone* is made possible by Canon. This program represents the largest corporate donation for wildlife conservation in the park.

Yellowstone Science
Yellowstone Center for Resources
PO Box 168
Yellowstone National Park, WY 82190

Change Service Requested

PRSRT STD AUTO
US POSTAGE PAID
National Park Service
Dept. of the Interior
Permit No. G-83

Support *Yellowstone Science*

Our readers' generosity helps to defray printing costs.

Make checks payable to the Yellowstone Association, and indicate your donation is for *Yellowstone Science*. Checks can be mailed to
Yellowstone Association
PO Box 117
Yellowstone National Park, WY
82190-0117

Thank you!

ANA HOUSEAL

STaRRS students document changes at Mammoth Hot Springs.

Yellowstone Science is available electronically at www.greateryellowstonescience.org/ys and in print. Readers may subscribe to the electronic and/or the print version. To update your subscription, email yell_science@nps.gov.