Porewater and Hydrothermal Vent Water Inputs to Yellowstone Lake, Wyoming

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Abstract

Geochemical inputs to Yellowstone Lake, Wyoming, come from a variety of sources, including hydrothermal vents, groundwater, rainwater, flux from sediments, and direct runoff. One-third of Yellowstone Lake is directly influenced by hydrothermal activity (hot-water vents and fumaroles). Geothermally heated water percolating through the chamber is highly enriched with carbonate, silicate, chloride, and methane, with some locations additionally rich in iron and sulfide. Vent waters in West Thumb typically contained sub-micromolar concentrations of Fe (iron), while those in Mary Bay and off Stevenson Island contained about 10 µM (micromolar). Water column concentrations of dissolved iron ranged from 250 to 450 nM (nanomolar) in Mary Bay, but were very low in the waters of Southeast Arm, West Thumb, and off Stevenson Island. Porewater and vent water chemistry provided evidence for lake water dilution of vents below the sediment–water interface. Significant fracturing of source water conduits was indicated by extreme differences in porewater profiles from cores less than 5 m apart in the geothermally vigorous West Thumb. Some samples approached theoretical reservoir composition for geothermally active areas of Mary Bay and West Thumb, showing chloride concentrations reaching several mM (millimolar), and, in the case of Mary Bay, extrapolate to the geothermal end member (~20 mM) at a depth of only 2–3 m. These steep concentration gradients support diffusive chloride fluxes across the sediment–water interface three orders of magnitude higher than those in non-venting depositional areas.

Introduction

Yellowstone Lake, Wyoming, is located in the caldera of the largest volcanic eruptions known, which occurred 1.2 million and 650,000 years ago at a mid-continental hot spot, rather than in the more widespread tectonic spreading centers. The Yellowstone hot spot has interacted with the North American plate for millions of years, causing widespread outpourings of basalt. Some of the basaltic melt, or magma, produced by the hot spot accumulates near the base of the plate, where its heat melts the rocks from the Earth's lower crust. As a result, the underlying structure is composed primarily of granite overlain by volcanic silica as opposed to freshly upheaved basalts. Geothermally heated water percolating through the relic chamber is highly enriched in carbonate, silicate, chloride, and methane; some locations are also enriched with iron, manganese, and sulfide. Yellowstone National Park is well known for its steaming geysers, shimmering thermal pools, and bubbling painted mudpots. Some of the greatest characteristics that are not visible are the hydrothermal vents submerged under Yellowstone Lake; hydrothermal activity in the form of springs and fumaroles are described by Remsen et al. (1990) and Marocchi et al. (2001).

The magma chamber encompasses the northern part of Yellowstone Lake, while the Yellowstone River inflow and the southern half of the lake (South and Southeast arms) are outside the caldera. Previous work has shown active hydrothermal venting (geothermal hot springs and fumaroles) in several areas of the lake, which strongly influences the chemical composition of the lake water (Cuhel 1998; Klump et al. 1988). This is also observed in deep-sea hydrothermal vents, where vigorous plumes mix with deep water (Butterfield et al. 1997; Cowen et al. 1986), but the large receiving volume defies budget closure, which is one of the goals of past work in Yellowstone Lake (Aguilar et al. 1999).

Previous investigations of thermal waters from the Norris–Mammoth corridor have used different approaches to identifying sources of hydrothermal fluids. These have included the use of natural isotope tracers (e.g., H, He, Li), elemental abundances (e.g., S, Cl, Na, Ca), and the number of dissolved species present (Fournier 1989; Palmer and Sturchio 1990; Kharaka et al. 1991; Bullen and Kharaka 1992; Fournier et al. 1992; Kharaka et al. 1992, Rye and Truesdell 1992; Sturicho et al. 1992; Lewis et al. 1997). Based on all these studies we can compare recent results with those performed several years ago in order to have a better understanding of the changing environment in the Yellowstone Lake area and other areas in the caldera.

The interactions of the geothermal systems with biology have an important role in understanding the processes of the origins of early life. The high-temperature systems may be relevant to understanding extreme environments on Earth as well as on other planets and moons in our solar system.

Study Area

Sampling sites on Yellowstone Lake. Yellowstone Lake is located in the southeast section of Yellowstone National Park, in an area with frequent tectonic activity. The lake comprises an area of 341 km^2 and it is the largest high-altitude lake in North America. The northwestern area of the lake lies inside the caldera, whereas the southern area as well as South and Southeast arms are located outside the caldera (Figure 1). Several areas have been sampled through the years, but all the collections mentioned in this paper were from 1998. There are areas with evident geothermal activity, such as Mary Bay, Sedge Bay, Steamboat Point, Stevenson Island, and West Thumb. All these areas have been sampled frequently, as have others such as the Yellowstone River inlet (located outside the caldera, Southeast arm) and outlet (inside the caldera).

Methods

Use of a remotely operated vehicle. The use of a remotely operated vehicle (ROV) is critical for general surveying of and sampling hydrothermal vent systems in Yellowstone Lake (Figure 2). The ROV designer and operator, Dave Lovalvo of Eastern Oceanics, is a former pilot of *DSRV Alvin* (deep sea research

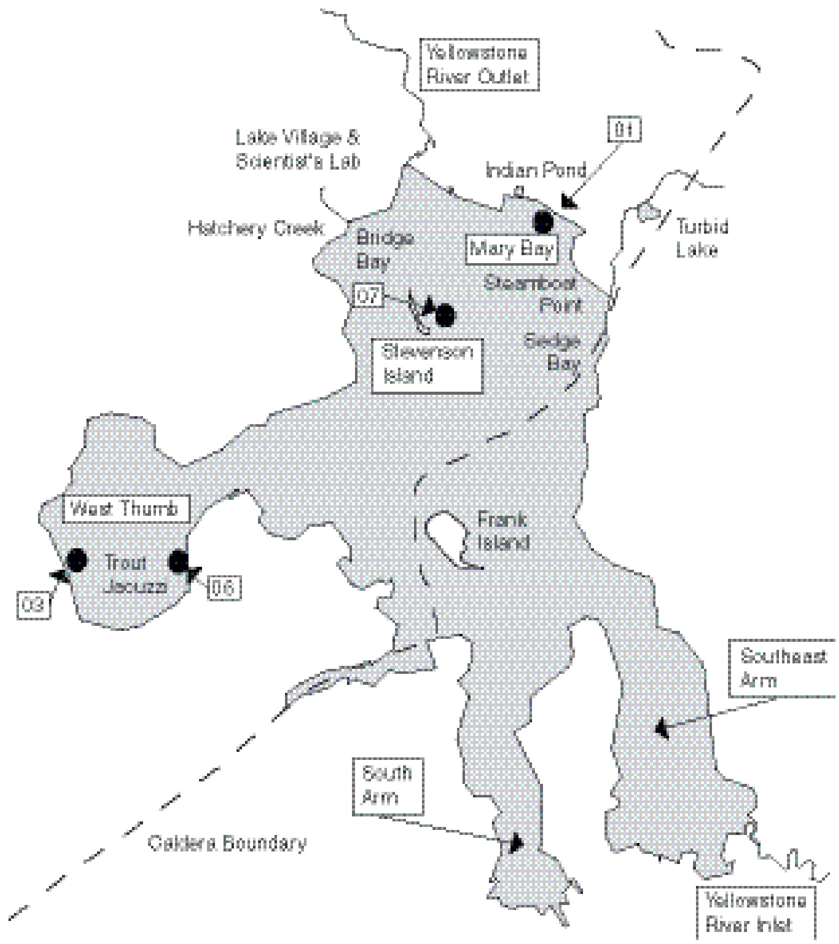

Figure 1. Map of Yellowstone Lake showing selected sampling areas: West Thumb, Mary Bay, Stevenson Island, Southeast Arm, and Yellowstone River inlet and outlet. The rim of the caldera is depicted by the dotted line. Core collection sites are in solid circles, as follows: 01 = Mary Bay 01 core, 03 = West Thumb 03 core, 06 = West Thumb 06 core, and 07 = Stevenson Island 07 core. Map from Marocchi et al. 2001; reproduced by permission.

vessel) and *ROV Jason*, and has produced a practical array of modular instruments for water and solid phase sampling, as well as cameras for still pictures and video (Buchholz et al. 1995; Klump et al. 1992). The areas of interest are hard to sample by conventional means. Visual observations of shimmering surface waters are always important clues to exploring the bottom of the lake. When looking for evidence of vents on the surface waters, we rely on vigorous bubbling that is visible from a distance on a calm day (Figure 3).

Field methods. Vent samples were collected with the ROV on board the *R/V Cutthroat*, using an articulated arm outfitted with a thermistor probe at the end to

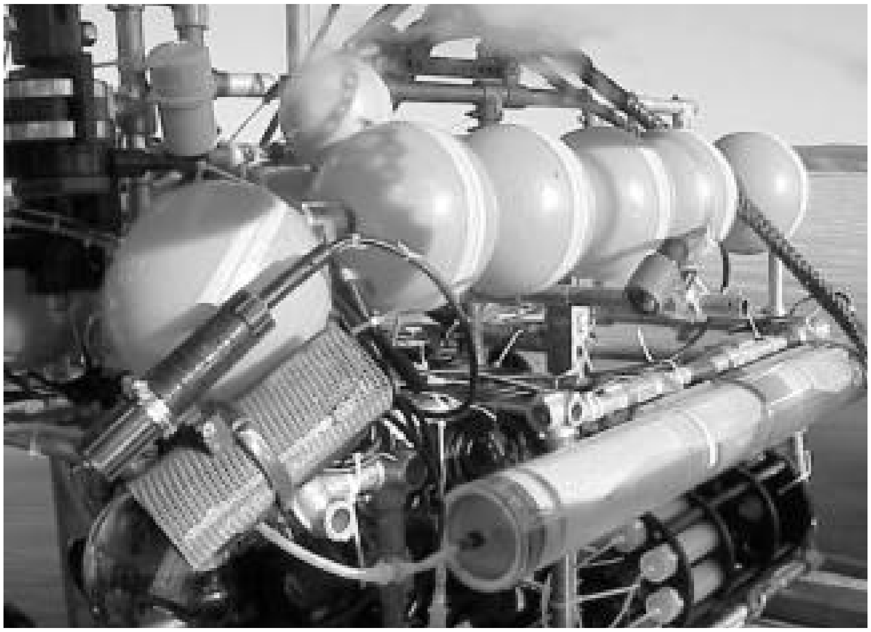

Figure 2. Remotely operated vehicle from Eastern Oceanics used to collect vent and bot - tom water.

Figure 3. Bubble field on surface waters of Mary Bay. On a calm day they can be seen from a distance. The bubbles are used to find new vent activity in different areas of the lake.

measure the temperature of the water as it was collected. Water was collected into 2-L polycarbonate syringes; samples were then retrieved and put into smaller, all-plastic syringes through a three-way valve. Samples were then transported in a cooler to the laboratory for analysis and preservation.

Cores were collected from the *Cutthroat* with a 3-inch Benthos gravity corer with cellulose acetate butyrate liners (Figure 4). Sediment was then transported to the laboratory and transferred with a hydraulic extruder to the Jahnke squeez-

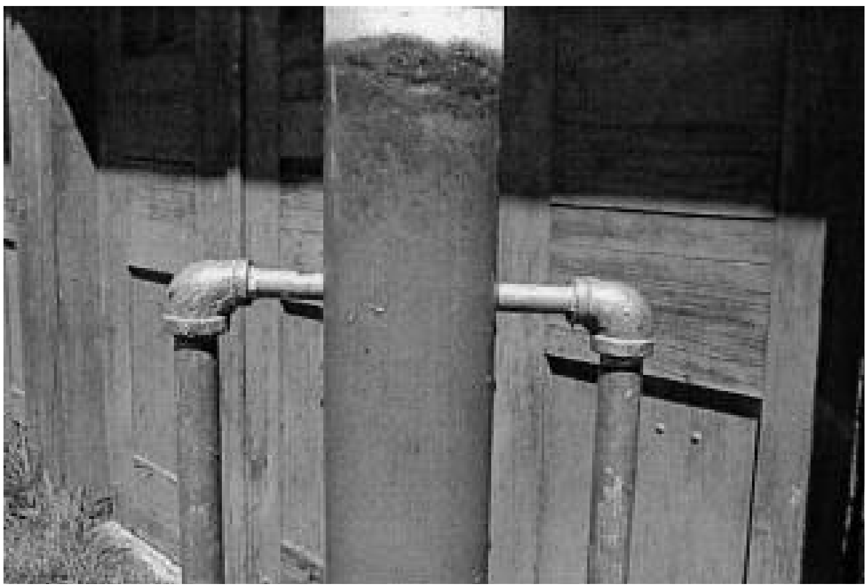

Figure 4. Core from West Thumb inside a core liner. Notice the darker sediment water–interface. This core is on the extruder, ready to be transferred into the squeezer liner.

er (Jahnke 1988) to subsequently obtain porewater (Figure 5). Porex inserts (a porous polyethylene rod to "guide" the water through while being pushed out by the action of the piston) were acid-washed and rinsed through many changes of E-Pure water (18-meg ohm/cm resistance) to zero residual chloride. The last rinses with E-Pure water were done in a Coy anaerobic chamber (90% N_2, 10% H_2) with water devoid of oxygen. All parts contacting the sample were acid-washed and those inserted were maintained anaerobically (in sealed serum vials) until the instant of use. The in-line 25-mm filters (0.2-µm pore size) used were ion chromatography-approved ultraclean commercial units (IC Gelman Acrodiscs), and all-polypropylene syringes received the sample. Components for reduced sulfur analysis were prepared in an anaerobic chamber, with dilution blanks, standards, and reagents in serum vials. Samples for trace metals were acidified with trace metal-certified nitric acid and stored in acid-washed polypropylene tubes. The samples for routine chemical analysis were stored at 4°C in polypropylene tubes. Core processing (sectioning, squeezing) was accomplished in a protected part of the National Park Service garage.

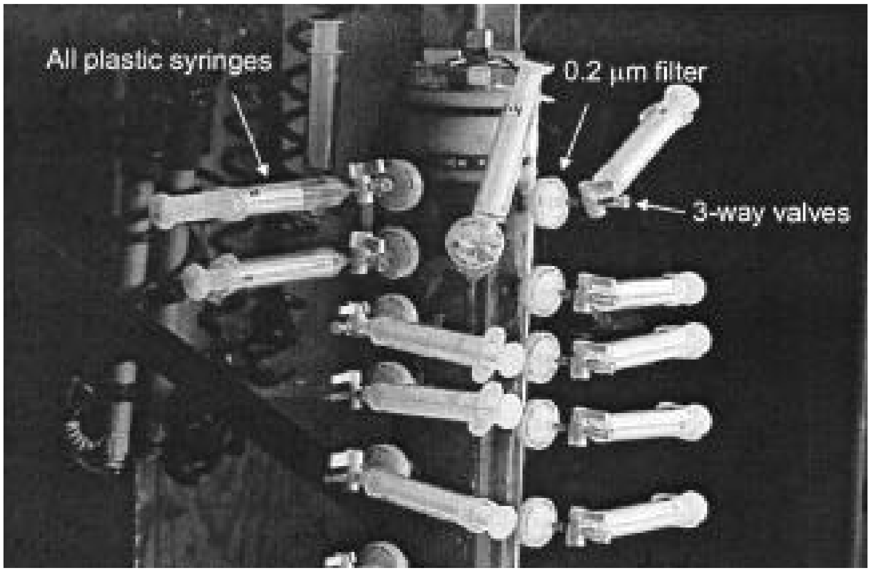

Figure 5. Porewater squeezer used to obtain porewater by applying pressure vertically; the water tends to be forced horizontally ("guided") by the porex inside the sediment at the end of the filter. The picture shows how the squeezer is put together, showing the depth intervals to obtain porewater from different depths in the core.

Chemical analyses. In the laboratory, samples were filtered through 0.2-µm filters (Supor, Nuclepore) and water was aliquotted for the different analyses. Dissolved mineral compounds were measured in the field laboratory by several methods: flow injection analysis (FIA; silicate, SiO_2), ion chromatography (IC: chloride, Cl^-, sulfate, $SO_4^=$), and spectroscopy (ammonium, NH_4^+), all according to standard methods (APHA 1992). Reduced and total iron was also determined in the field by the ferrozine spectrophotometric method of Stookey (1970), with (total iron) and without (reduced iron, FeII) reductant extraction. Total carbon dioxide, ΣCO_2, was analyzed by the Teflon–membrane flow injection method of Hall and Aller (1992). Reduced sulfur compounds (hydrogen sulfide, H_2S, thiosulfate, $S_2O_3^=$, sulfite, $SO_3^=$) were quantified by a scaled-up modification of the micro-bore high-performance liquid chromatographic (HPLC) method of Vairavamurthy and Mopper (1990), using dithio-bis-nitropyridine (DTNP) derivatization. The analytical equipment was transported to Yellowstone National Park, where all labile species were analyzed on site within one day of collection and analytical preparation.

Porewater flux was calculated from porewater concentration profiles, and concentration gradients at the sediment–water interface were used to calculate fluxes via Fick's first law of diffusion (Berner 1980): $J = D_S \cdot \phi \cdot dC/dz$, where J is the flux of the different components; D_S is the whole sediment molecular diffusivity corrected for tortuosity (Li and Gregory 1974); ϕ is the porosity at the sediment–water interface; and dC/dz is the slope of the concentration gradient.

Results

Porewater. Since almost a third of Yellowstone Lake is directly influenced by hydrothermal activity, it is important to measure chemical components that can provide a proxy for geothermal activity in the lake. Chloride is an important indicator of geothermal activity, and the Yellowstone River inlet provides a low-chloride concentration (<7 µM). The subsurface deep reservoir containing fluids that feed the thermal basins in Yellowstone National Park is thought to have concentrations of about 20 to 21 mM chloride (Truesdell et al. 1977; Fournier 1989).

Porewater profiles in Figures 6–12 depict distinct sites in Yellowstone Lake, with all cores being collected during the 1998 season. The Mary Bay 01 core (01-MB; shown as open squares in the figures) was taken from a vent field in the bay, and smelled of hydrogen sulfide as we brought it onto the vessel. This core was close to one that melted the plastic core liner (temperature >135°C) moments before. The West Thumb 03 core (03-WT; open circles) was collected near the West Thumb geyser basin. The West Thumb 06 core (06-WT; closed circles) was collected in the West Thumb deep basin. The Stevenson Island 07 core (07-SI; closed squares) was collected from the deep canyon east of the island (refer to locations in Figure 1).

Chloride is a conservative and non-reactive ion that is used as a geothermal tracer. Chloride concentrations in Mary Bay sediments reached 10 mM, the highest concentration measured in porewater (Figure 6). A concentration of about 5 mM was also found in a core from West Thumb; all the other sites measured showed a concentration lower than 1 mM.

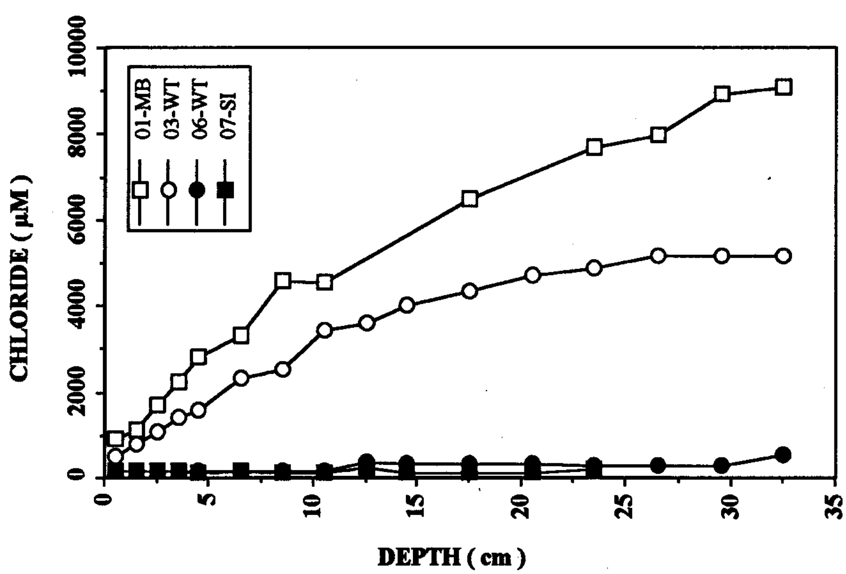

Figure 6. Porewater profile depicting chloride concentration (µM, micromolar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

Diatoms (algae) require silica to produce frustules (skeletons made of silica). These organisms can settle to the bottom of the lake by different processes; the frustules then begin to undergo dissolution. Evidence of this process is found in the porewater profiles from the sediments from different areas of the lake. Silica is a compound that is non-conservative and biologically reactive. Silicate reflects the diagenetic/dissolution control in the water and sediments, where decomposition takes place without geothermal influence. In addition, vent water seepage into sediments adds additional silicate, and there are some examples of porewater profiles that show this influence. Mary Bay 01 and West Thumb 03 had the highest concentrations, about 2.5 mM SiO_2, whereas non-geothermally influenced cores peaked at 1 mM (Figure 7). Silicate shows a higher concentration than expected from a diagenetically generated profile, showing the influence of vent activity in the area. The values for the Southeast Arm reach a concentration of 750 µM, similar to that of West Thumb 06 and Stevenson Island 07.

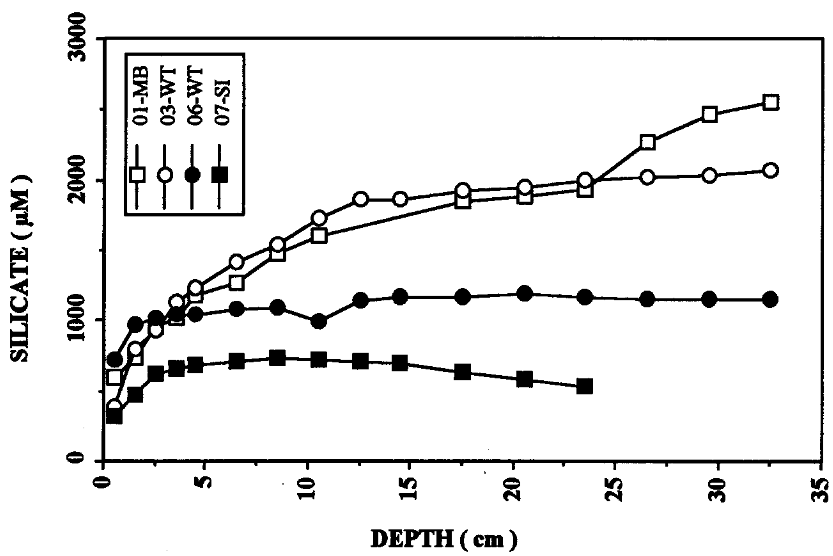

Figure 7. Porewater profile depicting silicate concentration (µM, micromolar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

Hydrogen sulfide is a compound that we refer to as the "smell of success" since it is a great marker for reducing conditions in sediments as well as vent water. It is a readily distinguishable reduced component that will be present in an area where there is usually little oxygen present. It is also a characteristic of geothermally derived vent waters. Sulfate reduction from bacteria is an important component in the production of this reduced compound. Except for methane, hydrogen sulfide is the most inefficient to produce. Hydrogen sulfide concentration was highest, 550 µM, in Mary Bay 01 (Figure 8). The concentration in the other cores was less than 10 µM, which is significantly lower than that in the active areas. Hydrogen sulfide has been found consistently in Mary Bay.

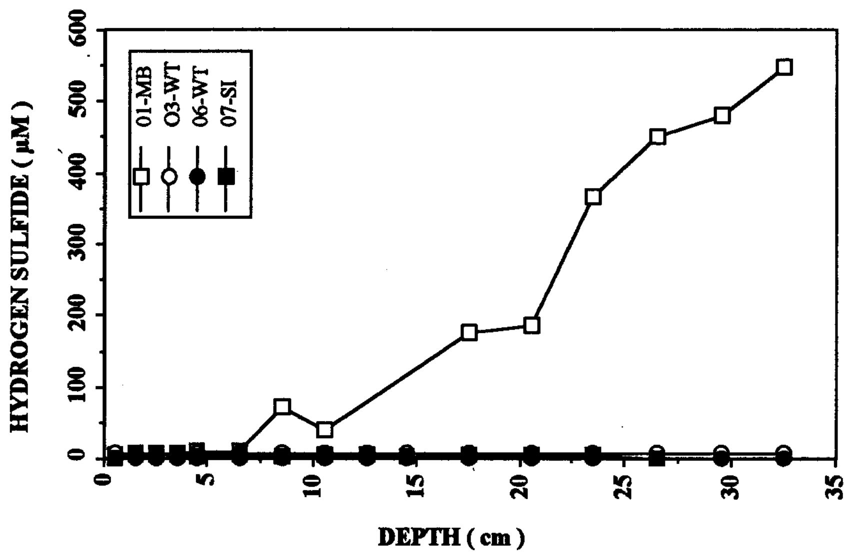

Figure 8. Porewater profile depicting hydrogen sulfide concentration (µM, micromolar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

Bacterial sulfate reduction is a process of organic matter decomposition, where sulfate is used as an energy source by bacteria, by which sulfate is reduced to hydrogen sulfide. Hence, sulfate reduction tends to decrease with water column depth because less organic matter reaches those sediments. This process occurs in the absence of oxygen. Sulfate was highest, 200 µM, at Stevenson Island, whereas the concentrations in the other cores were less than 80 µM (Figure 9). West Thumb 03 showed a very shallow gradient compared with the gradient from Mary Bay 01.

Reduced iron concentrations were highest in Stevenson Island 07, as well as in West Thumb 06; that core, taken from the deep basin, had a concentration of 37 µM (Figure 10). Iron laminations are found extensively in the West Thumb area. Typically, vent water lacks reduced iron in the effluent, but some areas in the sediment show evidence of iron oxides.

Ammonium is released to porewater from the decomposition of labile organic nitrogen compounds contained within the bulk of the organic matter deposited in sediments (2–4% organic carbon and 0.3–0.5% total nitrogen). Porewater concentrations of ammonium produced by organic matter decomposition can reach 600 µM in the high-deposition areas of the lake (Figure 11). Profiles observed in these locations are consistent with a diagenetic source, but the steep gradient measured in Mary Bay could result in part from geothermally influenced processes.

Though produced by organic matter decomposition, its main source of enrichment is the extraordinarily high concentrations (to 25 mM) in vent reservoir fluids. Carbon dioxide is another indicator of geothermal activity. High con-

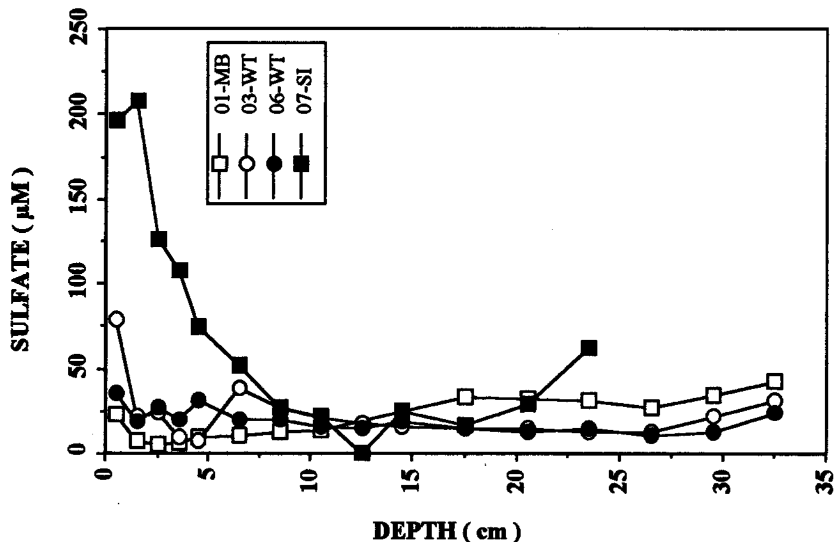

Figure 9. Porewater profile depicting sulfate concentration (µM, micromolar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

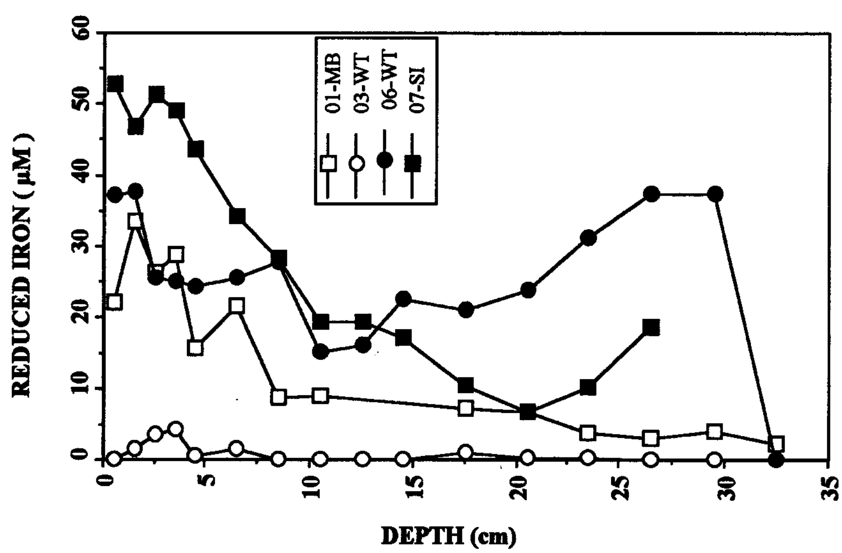

Figure 10. Porewater profile depicting reduced iron concentration (µM, micromolar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

centrations were measured in the Mary Bay 01 and West Thumb 03 cores (Figure 12), both showing evidence of active geothermal influence, based on the chloride concentration.

Vent water. Vents are very heterogeneous, with temperatures ranging from 20°C to 112°C and pH values from 4 to 8.6, as well as having chemistry that

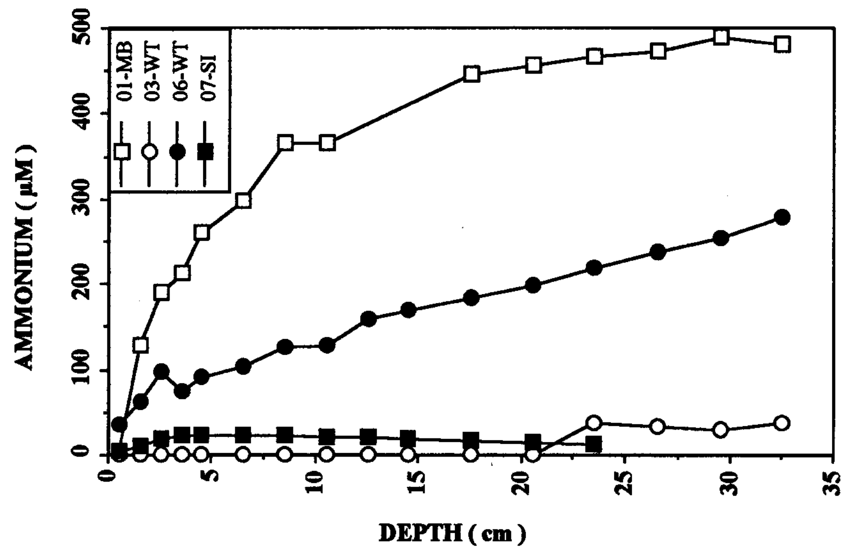

Figure 11. Porewater profile depicting ammonium concentration (µM, micromolar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

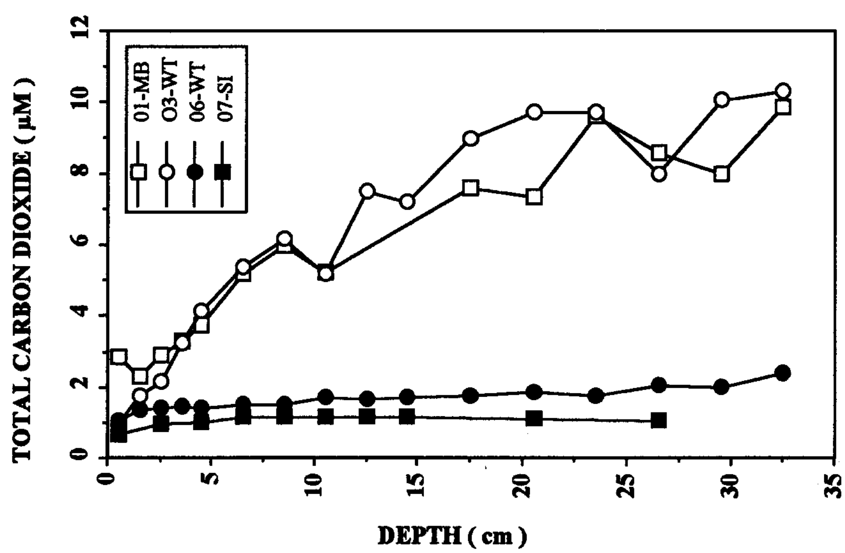

Figure 12. Porewater profile depicting total carbon dioxide concentration (µM, micro - molar) with depth in four different cores from Mary Bay, West Thumb, and Stevenson Island.

varies with location. Chemical differences from vents in different areas have allowed us to group the different characteristics into domains (see Cuhel et al., this volume). Vent waters from West Thumb and Mary Bay showed enrichment in chloride and silicate, although they were highly variable (Table 1). Reduced iron was present in vents from Stevenson Island and Mary Bay, where the reduced species can remain in the water for at least 24 hours (data not shown).

Lake water. Lake water collected in a deep vent area (near Stevenson Island) showed chemical enrichment in several constituents—chloride, silicate, sulfate, sodium, etc.—when compared with surface water collected at the Southeast Arm inlet and the Yellowstone River outlet (Table 1). When lake water values were compared with those of vents of the different areas, it becomes evident that, for

Table 1. Selected chemistry of Yellowstone National Park vents, Yellowstone River inlet and outlet, and water column values.

Location	pH	Cl (µM)	Fe (µM)
WT vents	5.5–8.6	50–1,147	<0.18–0.54
MB vents	4.9–5.9	144–169	0.23–9.3
SI vents	5.0–6.2	136–148	1.7–8.1
SE Arm water column	7.45	120	<0.18
WT water column	7.3	154	<0.18
MB water column	6.75	179	0.25–0.45
SI water column	7.4	141	<0.18
YR-inlet	7.05	7	0.5
YR-outlet	7.29	126	0.197

MB = Mary Bay, SI = Stevenson Island, WT = West Thumb, YR = Yellowstone River

example, Mary Bay has water that still reflects the hydrothermal composition of the vents.

There were distinct differences in the composition of hydrothermal vent fluids from different parts of Yellowstone Lake. For example, vents from the West Thumb area were rich in chloride but poor in sulfur compounds, as compared with vents from Stevenson Island which were rich in sulfur but poor in chloride. In contrast, chimney structures from these vents record times that the vent fluids must have been different in composition because they contain precipitates that could not have formed from the vent fluids that currently emanate from these sites; chimney structures from Stevenson Island contain sulfur crystals as well.

Flux from the sediment into the overlying water can be calculated from the porewater chemistry from Mary Bay, West Thumb, and Stevenson Island. Table 2 shows the calculated flux from chloride as the geothermal activity tracer, and silica as the dissolution/diagenetic control in porewater. Chloride flux was highest (two orders of magnitude) from the Mary Bay and West Thumb hot cores; other cores and areas such as Stevenson Island as well as Southeast Arm (which is outside the caldera) do not provide chloride to the receiving lake water. Silica does not show such a dramatic difference, but the same cores have high standing silica concentrations throughout, probably controlled by the solubility of amorphous silica (diatoms) which makes up to ~50% of the sediment mass.

Table 2. Porewater concentrations and flux from cores obtained in Mary Bay, West Thumb, Stevenson Island, and Southeast Arm, showing values for chloride, a "geothermal tracer," and silica, a "dissolution/diagenetic control" parameter.

Station Porewater chemistry	Chloride "geotheramal tracer" [conc] @ z = ∞ mmol/L	Chloride Grad µM cm^{-1}	Chloride Flux Mol $m^{-2} y^{-1}$	Silica "dissolution/diagenetic control" [conc] @ z = ∞ mmol/L	Silica Grad µM cm^{-1}	Silica Flux Mol $m^{-2} y^{-1}$
Mary Bay "hot" core	12.5–20.0	450	2.41	2,000	200	0.80
W. Thumb "hot" core	7.5	360	1.93	2,050	224	0.90
W. Thumb	0.185	5.5	0.017	1,200	165	0.47
Stevenson Island	0.180	-0.6	-0.002	720	311	0.89
Southeast Arm	0.172	0.34	0.001	900	140	0.40

Discussion

Geochemical inputs to Yellowstone Lake come from a variety of sources, namely: hydrothermal vents, groundwater, rainwater, flux from sediments, and direct runoff (including from tributaries). Approximately one-third of the lake is directly influenced by hydrothermal activity through hot-water vents and fumaroles. Surveys of lake water, vent water, and sediment porewater gradients established zones of direct and subsurface inputs of geochemically altered fluids. Vent water intrusion into the surrounding sediments is evident in some of the profiles. In some instances, chloride approaches theoretical reservoir concentrations (20 mM) and the silicate concentration at depth seems greater than that expected from diagenesis alone. Porewater and vent water chemistry provides evidence for lake water dilution of vents below the sediment–water interface.

Reduced sulfur compounds are important components of the vent waters in Mary Bay and Stevenson Island, while in the West Thumb these compounds were usually undetectable. The vent fluids exhibit a highly variable concentration of dissolved minerals in different areas of the lake as well as for different years of sampling. This is shown, for example, in the solid phase from West Thumb (Figure 13), where highly laminated iron–manganese oxide crusts are found in areas that typically do not contain sulfide, methane, or other reduced compounds.

Strong evidence for vent fluid seepage was found in the hot-core porewater measurements of chloride (10 mM), total CO_2 (to 11 mM), and silicate (2.8 mM), all highly enriched in deep reservoir fluids. Some areas of the lake contain high concentrations of sulfide (500 µM) and of iron (50 µM). Because inorganic nitrogen (ammonium) is virtually absent from the water column and vent fluids, diagenetic production of ammonium from organic matter may provide more growth-

Figure 13. Solid phase sample collected from West Thumb. Note the laminations on the surface of alternating manganese and iron oxides.

promoting habitats in surrounding sediments than in aqueous environments.

One of the factors that may have influenced the vent activity throughout the lake was the lake stage or water level, which directly affects the hydrostatic pressure on vent systems. There seemed to be a correlation between high activity in the vents when water levels were low, and low activity when water levels were high. This is one of the factors that will benefit from long-term studies of the different vent areas in the lake.

Comparing data from the inlet of the Yellowstone River (in Southeast Arm) and its outlet (in the northern part of the lake), it is clear that there is a significant hydrothermal influence in the lake (Figure 14). Chloride is virtually absent in the inlet waters. Hence, much higher values of lake water provide strong evidence for an external source of the ion. During three years of piezometer studies to measure the groundwater inputs to the lake, we concluded that the source is not sufficient to explain the lake water enrichment. Chloride, then, contributes another piece of evidence that points to a geothermal influence in the concentration of key components (see Klump et al., this volume). There are also sources and sinks of other elements, but having mentioned just a few we can see that this is a very dynamic geoecosystem, in which different sources of chemicals are found and where microbiology is an important component.

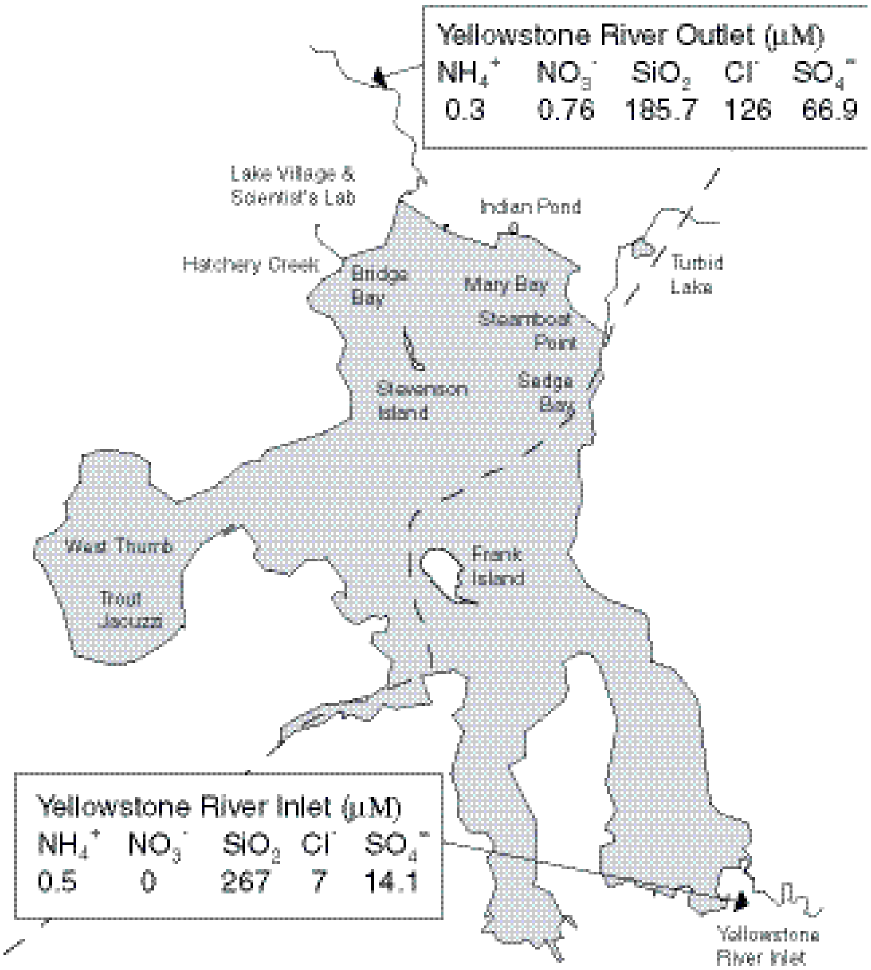

Figure 14. Yellowstone Lake map showing different concentrations of selected compounds and the changes incurred from the source of the water coming into the lake outside the caldera region to the Yellowstone River outlet.

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Yellowstone Lake Cutthroat Trout Hemoglobin Polymorphism

Jeffrey Carl Braman

Abstract

Hemoglobin polymorphism was observed in Yellowstone Lake cutthroat trout. Variation occurred only in the cathodally migrating hemoglobin components. Eight of the ninety-three trout sampled displayed an electrophoretic pattern identical to that of adult rainbow trout.

Introduction

Data presented in this paper were published previously (Braman et al. 1980). The text is extensively revised with additional references cited to support the contention that hemoglobin polymorphism is a unique characteristic of Yellowstone Lake cutthroat trout.

Yellowstone Lake cutthroat trout *(Oncorhynchus clarki bouvieri)* represent a "keystone species" in the Yellowstone Lake ecosystem (Plumb and Koel 2001). Bald eagle *(Haleaeetus leucocephalus),* white pelican *(Pelecanus occidentalis),* osprey *(Pandion haliaetus),* otter *(Lutra canadensis),* black bear *(Ursus ameri - canus)* and grizzly bear *(Ursus arctos)* prefer cutthroat trout to exotic lake trout *(Salvelinus namaycush)* as a food source (Plumb and Koel 2001). Piscivorous lake trout, discovered in Yellowstone Lake in 1994, and the Whirling Disease parasite, found in several Yellowstone Lake cutthroat trout in 1998, threaten to collapse the cutthroat trout population (Koel et al. 2001). Decimation of cutthroat trout may result in a "catastrophic shift" to an altered Yellowstone Lake ecosystem state that would require drastic and expensive intervention for restoration (Scheffer et al. 2001). Scheffer et al. propose that "building and maintaining resilience of desired ecosystem states is likely to be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change."

Building resilience into the Yellowstone Lake ecosystem might involve propagating Yellowstone Lake cutthroat trout variants that demonstrate increased resistance to the Whirling Disease pathogen and/or improved survival rate following bursts of vigorous physical activity when avoiding predators and during spawning. Identifying variants possessing biochemical systems with unique properties that confer survival advantage under extremes of physical activity is the research emphasis described in this paper. Studying the underlying molecular and physiological mechanisms responsible for improved fitness is the ultimate goal of this research.

Hemoglobin is a biochemical system adapted to bind and release oxygen under a wide range of environmental and physiological conditions (Hochachka and Somero 1973), allowing fish to exploit a variety of habitats and adapt to adverse conditions. Therefore, Yellowstone Lake cutthroat trout expressing hemoglobin with unique oxygen-binding properties might demonstrate increased resiliency to the extremes of physical activity described above.

Multiple Hemoglobin Components in Cutthroat and Rainbow Trout

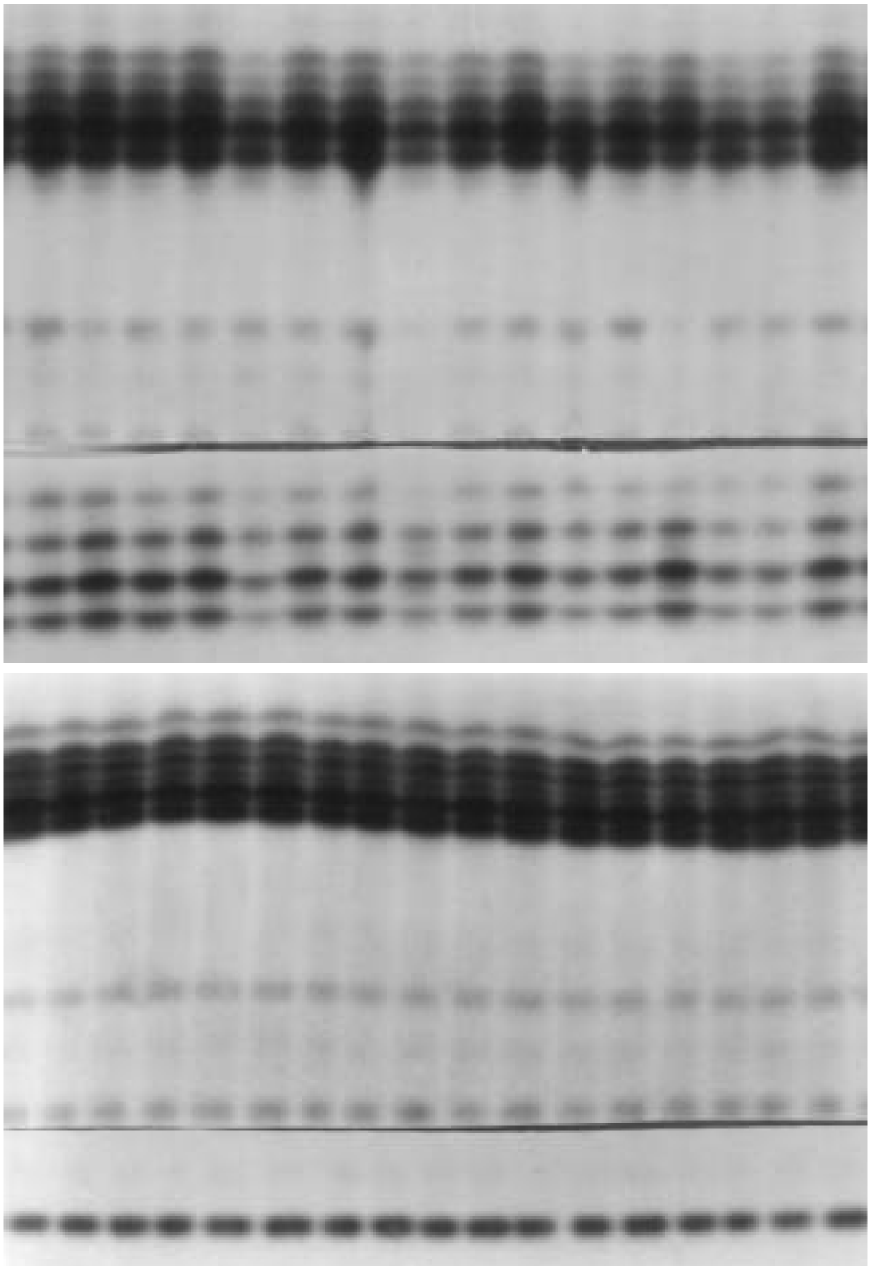
Multiple hemoglobin components in fish is a well-documented phenomenon, with cutthroat trout having twelve (Figure 1a) and rainbow trout having nine (Figure 1b) hemoglobin components (Braman et al.1977). A high-resolution starch gel electrophoresis method was developed to resolve eight negatively charged hemoglobin components from both species, all of which migrate coincidentally toward the positive electrode (anode). Rainbow trout have one and cutthroat trout have four positively charged hemoglobin components migrating toward the negative electrode (cathode). The single positively charged rainbow trout hemoglobin component migrates coincidentally with one of the four positively charged cutthroat trout hemoglobin components.

Hemoglobin Polymorphism in Yellowstone Lake Cutthroat Trout

Hemoglobin polymorphism due to allelic variation (Sick 1961; DeLigney 1969; Fyhn and Sullivan 1974; Fyhn and Sullivan 1975; Bonaventura et al. 1975; Perez and Rylander 1985; Giles and Rystephanuk 1989; Fyhn and Withler 1991) and ontogenetic variation (Wilkins 1968; Iuchi and Yamagami 1969; Giles and Vanstone 1976; Koch 1982; Wilkins 1985; Giles and Rystephanuk 1989) has been described in a variety of fish species, but not in cutthroat trout. Several cutthroat trout populations in the Intermountain West were examined for hemoglobin polymorphism by the starch gel electrophoresis method described above. All fish demonstrated the prototypical cutthroat trout phenotype with twelve hemoglobin components (Figure 1a). Yellowstone Lake cutthroat trout collected from the Peale Island area were also examined for hemoglobin polymorphism. Blood samples were collected on two occasions (September and October 1974) from a total of ninety-three fish. Variation in hemoglobin components migrating toward the cathode was observed in fish collected on both occasions (Braman et al. 1980; Figure 2). The polymorphism is complex in that there are concentration differences in hemoglobin components within a given sample in addition to variation in the number and concentration of hemoglobin components between samples. It is interesting to note that eight of the ninety-three fish sampled possessed the rainbow trout phenotype, with a single hemoglobin component migrating toward the cathode. These fish were not, by all apparent outward characteristics, cutthroat–rainbow (cuttbow) hybrids.

Additional Observations Made of Yellowstone Lake Cutthroat Trout

Fish sampled near Peale Island appeared to be adults ranging in size from 30 to 40 cm in length. Many of the fish were infested with unidentified ectoparasites on the body and, in particular, on the fins, where considerable damage was inflicted. A third sample of 50 cutthroat trout was collected one year later (1975)



Figures 1a and 1b. Starch gel electrophoresis of adult cutthroat trout (1a) and adult rain - bow trout (1b) hemoglobin components. Electrophoresis was performed as described in Braman et al. (1976). The anode (positive electrode) of the electrophoresis chamber is located at the top of the photo. The visible horizontal line running across the width of the gel in the photo represents the origin where hemoglobin samples were applied.

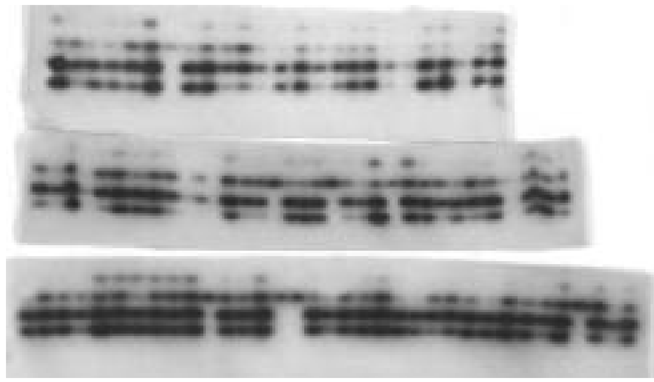


Figure 2. Three starch gel sections showing hemoglobin components migrating toward the cathode (negative electrode). Samples are from 93 adult Yellowstone Lake cutthroat trout. Electrophoresis was performed as described in Braman et al. (1980). Each section is oriented so that the origin is positioned at the top and the cathode is positioned at the bottom of each segment.

from a site approximately five miles north of Peale Island. These fish were also 30 to 40 cm in length, were not infested with ectoparasites, and did not demonstrate hemoglobin polymorphism. This second group of Yellowstone Lake cutthroat trout had the characteristic phenotype (i.e., having twelve hemoglobin components) shown in Figure 1a.

Plausible Explanations for the Observed Hemoglobin Polymorphism

Observed protein variation when using starch gel electrophoresis may result from artifacts generated during sample preparation and storage (Utter et al. 1974; Reinitz 1976). This is an unlikely explanation for hemoglobin polymorphism in Yellowstone Lake cutthroat trout because variation occurred exclusively in the hemoglobin components migrating toward the cathode. Hemoglobin components migrating toward the anode did not vary in number and concentration. If sample preparation and storage caused the polymorphic hemoglobin electrophoretic patterns, then all hemoglobin components from every population of fish would likely demonstrate variation, not just the hemoglobin components migrating toward the cathode, as in the Peale Island group of Yellowstone Lake cutthroat trout. In practice, identical electrophoretic patterns were obtained with freshly prepared and three-week-old hemoglobin samples. A hemoglobin sample stored longer than three weeks demonstrated degradation of all hemoglobin components, as evidenced by streaking of the entire electrophoretic pattern.

Another explanation for hemoglobin polymorphism in Yellowstone Lake cutthroat trout is ontogenetic variation (Wilkins 1968; Iuchi and Yamagami 1969; Giles and Vanstone 1976; Koch 1882; Wilkins 1985; Giles and Rystephanuk 1989). This hypothesis is unlikely because all fish examined appeared to be adults, 30 to 40 cm in length.

Hemoglobin polymorphism in Yellowstone Lake cutthroat trout could be attributed to allelic variation and is complicated by the fact that rainbow trout genetic material was introduced into the Yellowstone Lake cutthroat trout gene pool as a result of stocking prior to 1915 (Jack L. Dean, personal communication). Allelic variation in cathodal hemoglobin components has been described for Arctic charr *(Salvelinus alpinus;* Giles and Rystephanuk 1989) and in anodal hemoglobin components for chinook salmon *(Oncorhynchus tshawytscha;* Fyhn and Withler 1991). Allelic variation resulting in polymorphic hemoglobin components of Yellowstone Lake cutthroat trout has not been confirmed. Breeding Yellowstone Lake cutthroat trout having known hemoglobin phenotypes, as well as performing crosses of Yellowstone Lake cutthroat trout with rainbow trout and scoring the phenotypes of the resulting offspring, will establish if the polymorphism is genetically based.

A further influence of rainbow trout genetic material on phenotypic expression of Yellowstone Lake cutthroat proteins is worth mentioning. The extent of introgression of anadromous rainbow trout *(Oncorhynchus mykiss irideus)* and coastal cutthroat trout *(O. clarki clarki)* was recently investigated by screening populations of these fish with amplified fragment length polymorphic (AFLP) and mitochondrial (mt) DNA markers (Young et al. 2001). Results of this work confirm that rainbow–cutthroat F_1 hybrids are produced from females of both species. Rainbow and cutthroat backcross hybrids were also detected, indicating that F_1 hybrids mate successfully with both rainbow and cutthroat parents. Hybrids were not found in all populations sampled and hybrid swarms were not evident. The data are consistent with the hypothesis that complete introgression of these two species is not possible due to an environment-dependent reduction in hybrid fitness. Screening Yellowstone Lake cutthroat trout with AFLP and mt DNA markers will aid in determining the extent and persistence of rainbow trout introgression due to stocking that occurred many years ago. AFLP markers are sensitive for identifying rainbow trout genetic material in cutthroat trout populations because, for the markers used by Young et al., rainbow trout did have cutthroat trout-diagnostic AFLP markers, while native cutthroat trout did not display any rainbow trout-diagnostic AFLP markers. Limiting the extent of introgression does not eliminate the possibility that Yellowstone Lake cutthroat trout harbor remnant rainbow trout hemoglobin alleles.

A second piece of circumstantial evidence obtained using a different experimental approach further reduces the importance of rainbow trout influence. Two-dimensional gel electrophoresis of serum proteins was used to distinguish native rainbow and cutthroat trout from cuttbow hybrids (Rourke and Wallace 1978). Results of these experiments show that serum protein profiles are different for native rainbow and cutthroat trout, but are equivalent for cuttbow and native cutthroat trout, suggesting that rainbow trout genetic material does not measurably alter the expression pattern of native cutthroat trout serum proteins.

Physiological stress represents another plausible explanation for the observed polymorphic hemoglobin patterns (Utter et al. 1974; Koch 1982). Circumstantial evidence in favor of this explanation is that Peale Island fish were infested with ectoparasites and had polymorphic hemoglobin components, while fish collected one year later five miles north of Peale Island were not infested with ectoparasites and did not have polymorphic hemoglobin components. However, a mechanism is lacking that links stress with variation in Yellowstone Lake cutthroat trout hemoglobin components migrating toward the cathode, and with the fact that several fish expressed the characteristic rainbow trout phenotype (i.e., having nine hemoglobin components).

Future Research

Cutthroat trout, rainbow trout, and other salmonids contain multiple hemoglobins that are divided into two groups. The anode group migrates toward the positive electrode during starch gel electrophoresis and contains hemoglobin components with relatively low isoelectric points. They are characterized by oxygen equilibria that are strongly dependent on pH, temperature, and ATP (adenosine triphosphate). The cathode group migrates toward the negative electrode during starch gel electrophoresis and contains hemoglobin components that are largely unaffected by pH, temperature, and ATP (Southard et al. 1986). Analogous anode and cathode groups of hemoglobin components are found in other teleost fishes, and it is hypothesized that the cathode group allows efficient uptake of oxygen at the gills as blood pH lowers during and following strenuous exertion (Powers and Edmundson 1972). Yellowstone Lake cutthroat trout demonstrate polymorphism in the cathode group of hemoglobin components. The physiological significance of this phenomenon deserves further investigation.

Yellowstone Lake cutthroat trout collected near Peale Island, many of which were infested with unidentified ectoparasites, demonstrated hemoglobin polymorphism. Fish sampled from a location approximately five miles north of Peale Island were not infested with ectoparasites and did not demonstrate hemoglobin polymorphism. It will be instructive to investigate whether hemoglobin polymorphism is a widespread occurrence in Yellowstone Lake cutthroat trout or if it is limited to fish confined to certain locations.

It is also important to establish whether hemoglobin polymorphism in the lake's cutthroat trout is due to allelic variation or is the result of stress.

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Underwater Domains in Yellowstone Lake Hydrothermal Vent Geochemistry and Bacterial Chemosynthesis

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J. Val Klump, and David Lovalvo

Abstract

Reduced inorganic compounds of geothermal-origin hydrogen sulfide (H_2S), iron (Fe[II]), and methane (CH_4) were common but not ubiquitous components of hydrothermal vent fluids of Yellowstone Lake at concentrations capable of supporting chemolithoautotrophic (geochemical-oxidizing, carbon dioxide (CO_2)-fixing) bacterial growth. Closely linked to the presence of reduced geochemicals was abundance of chemosynthetic bacteria and dark CO_2 fixation activity. Pronounced productivity at vent sites in the northern basin (Mary and Sedge Bays, Storm and Steamboat Points, and east of Stevenson Island) was accompanied by reduced sulfur stimulation in near-vent receiving waters, while none of these characteristics were found in West Thumb vent fields. Per-liter bacterial productivity at vents (to 9.1 µgC/L/hour) could reach algal photosynthesis in surface waters (to 8.9 µgC/L/hour). Thermophilic (heat-loving) sulfur- and methane-oxidizing bacteria were isolated from vent orifice waters, and CO_2 fixation incubations at 50°C indicated that the majority of chemosynthesis within the vents themselves was optimal at high temperatures. Receiving waters had much less activity at 50°C than at ambient temperature (4–20°C), distinguishing populations of mesophilic (moderate-temperature) bacteria that had also responded to the input of geochemicals from vents. Strong evidence for mineral-dependent bacterial productivity was obtained, with limited data suggesting an influence of lake stage or outflow on vent and productivity characteristics.

Introduction

For decades the colorful mats of bacteria and algae surrounding bubbling vents and fumaroles at Yellowstone National Park have been a focus of both touristic and scientific interest. It is with no small wonder that people look upon the growth of microorganisms in the often very hot, very corrosive fluids. Yet the interaction of biology with geothermal and geochemical energy may be more ancient than any other ecology. Prior to the mid-1970s, many scientists favored the theory of organic matter formation in the atmosphere and initial biological activity in surface brine pools using lightning energy as the primary catalyst (c.f. Miller 1953; Oro et al. 1990). Following the discovery of deep-sea hydrothermal geoecosystems in the mid-1970s, an additional hypothesis was developed, invoking organic matter formation and biological assembly in the high-temperature (to

350°C), high-pressure (>200 atm) deep-sea vents and surroundings. Both theoretical and experimental evidence supporting each theory exist, and in fact the two concepts are not mutually exclusive.

Early life certainly was microbial, at least tolerant of high temperatures, and predominantly made use of chemical energy for metabolic needs. At present, the highest temperatures for growth range to 113°C (Stetter 1999) and the isolated organisms are involved in methane and sulfur transformations. Yellowstone National Park offers a variety of habitats from hot (but <96°C), dissolved geochemical-laden (often to saturation with silicate or carbonate) surface springs and geysers with high microbial diversity (Barns et al. 1994) to hotter (to 130°C), dissolved geochemical-rich (but not saturated) waters and gases of Yellowstone Lake underwater vents and fumaroles. From a biogeochemical and ecological point of view, Yellowstone Lake is appealing because observed maximum vent-fluid temperatures range around or just above the limits for microbial life (Huber et al. 1989; Jørgensen et al. 1992), yet many of the same physical and geochemical characteristics of marine vents are preserved. Other freshwater hydrothermal sites have been identified, including massive sulfide deposits in Lake Tanganyika, East Africa (Tiercelin et al. 1989, 1993); hot-water vents in Lake Baikal, Russia (Crane et al. 1991; Shanks and Callender 1992), and deep microbial mats in Crater Lake, Oregon, USA (Dymond et al. 1989). Given the geochemically derived source of nutrition and the typically harsh physicochemical habitats in which they thrive, it is understandable that the bacteria known as lithotrophs (literally "rock eaters") are usually the dominant forms of life in such environments. While they provide further rationale for the study of freshwater systems, few are as tractable as Yellowstone Lake for accessibility to study.

The Yellowstone caldera underlies the northern half of Yellowstone Lake, while the Yellowstone River inflow and the southern half of the lake lie outside the caldera boundary. Within the caldera, geothermally heated subsurface water percolating through hot rocks above the magma chamber becomes enriched in carbonate, silicate, and chloride, with some locations additionally rich in methane, iron and sulfide. The park is world-renowned for its geothermal activity. This provides a significant opportunity to delineate vent geochemical effects on bulk lake water composition, because enrichment occurs far from the most significant surface inflow, which is the Yellowstone River in the Southeast Arm (Figure 1). The northern half of Yellowstone Lake is strongly influenced by underwater geothermal hot springs and gas fumaroles. These features release water with high concentrations of silicate and bicarbonate as well as reduced materials of mineral origin, including hydrogen sulfide, Fe[II], methane, and, more rarely, ammonia into the bottom waters. While the vents of Yellowstone Lake resemble deep-sea hydrothermal systems in some important respects, the nearly closed nature of the basin and the relatively small volume of receiving waters provides additional opportunities for process research. Because riverine inputs and outputs may be estimated, Yellowstone Lake geothermal and biogeochemical activities are amenable to budgeting by mass balance (inputs + change = outputs).

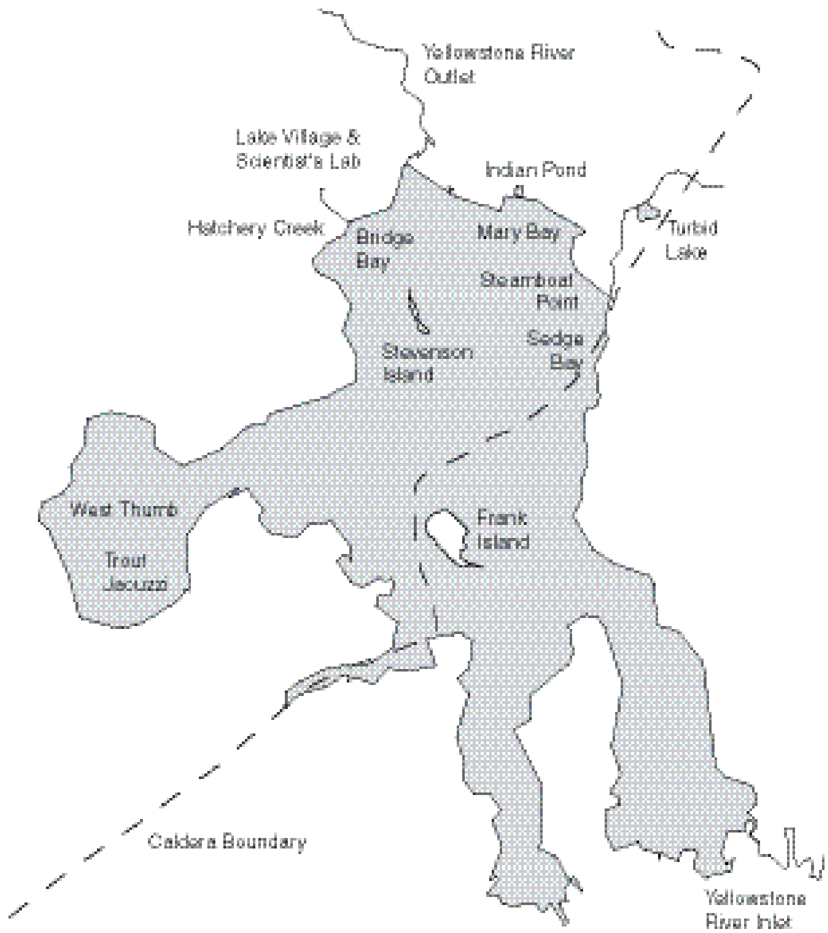

Figure 1. Map of Yellowstone Lake showing areas of underwater hydrothermal features sampled by ROV. West Thumb samples ring the entire basin, and Mary Bay, Sedge Bay, Steamboat Point, and Storm Point samples were also within 300 m of shore. Stevenson Island collections were made in the deep canyons just east of the island. Southeast Arm samples were taken midway down the arm (65–90 m water depth). Yellowstone River inlet samples were taken by NPS personnel well upstream of the mouth.

Work over the last 10 years on the development of remotely operated vehicle (ROV) survey and sampling technology (Marocchi et al. 2001; Remsen et al., this volume) demonstrated the absolute necessity of remote sampling of the deep, hot, seemingly inhospitable fluids of Yellowstone Lake vents. Starting with a simple Mini-Rover system consisting of video and still cameras and a claw with small pump-driven sipper tube, photographic surveys and water samples suitable for limited dissolved geochemical (Cl^-, SiO_2, $SO_4^=$, Na^+, etc.) and dissolved gas (CH_4, CO_2, ^{222}Rn) analysis were obtained (Klump et al. 1988). Combining the submersible results with surface-collected samples from the inlet at Southeast

Arm and the outlet at Fishing Bridge, it became apparent that aqueous species and gases found in vent fluids were also significantly enriched in lake water relative to surface inflows (Table 1) and in some cases comparable to marine venting systems. Although near-surface groundwater may contribute to enrichment, exceptionally strong signals from such geochemical indicators as radon-222 (derived from deep-rock degassing) and high flux rates of methane across the air–water interface imply a major role for submarine vents and fumaroles.

Table 1. Mineral content of mid-Atlantic Ridge seawater and marine vents compared with Yellowstone Lake inflow, outflow, and freshwater vents, 1994–1998 sampling results.

Parameter	Units	Maximum or Minimum	Marine Hydro-thermal Fluids (TAG, 26°N)[a]	Mid-Atlantic Seawater[a]	Yellowstone River Inflow	Yellowstone Lake Vent Fluids	Yellowstone River Outflow
Temperature	°C	Maximum	365	2	22	120	20
Acidity	pH	Minimum	3.35	7.8	7.05	4.92	7.29
Dissolved oxygen	mg/L	Minimum	0	7.6	9.0	0	8.5
Hydrogen sulfide	mM	Maximum	3.5	0	0.0004	0.9	0.0006
Sodium	mM	Maximum	537	464	0.078	3.360	0.341
Potassium	mM	Maximum	17.1	9.8	0.022	0.076	0.034
Calcium	mM	Maximum	0.031	0.01	0.093	1.032	0.136
Magnesium	mM	Minimum	0	52.7	0.057	0.025	0.087
Silica	mM	Maximum	20.75	0.2	0.333	1.283	0.223
Chloride	mM	Maximum	636	541	0.007	1.146	0.126
Sulfate	mM	Minimum	0	27.9	0.012	0.054	0.070
Manganese (II)	µM	Maximum	680	0	<0.20	0.87	<0.20
Iron (II)	µM	Maximum	5590	0.0015	<0.02	15	0.05

[a] Marine data from summary of Humphris and McCollom 1998.

Visual evidence of a long history of submarine geothermal activity is abundant in West Thumb, Mary Bay, Sedge Bay, Steamboat Point, and even in the very deep waters (120 m) off Stevenson Island, all within the caldera boundary (Marocchi et al. 2001). “Vent hole with white ppt. (323'); large relic pipe (176'); sponge attached to relic structure (176'); sulfide seeps, white ppt. (106'); bacterial mat on relic (110'); hot water vent with leeches (143'); sulfide fumaroles with white ppt. (143'); shimmering water with zooplankton swarm (310'); fish near hot water vent (128'); probe in 120°C hot vent—black smoker! (131')” are a few of the annotations from still and video images catalogued from the last few years (Remsen et al., this volume).

Submersible observations reveal some significant similarities and some major differences between the freshwater Yellowstone Lake hydrothermal systems and marine deep-sea hydrothermal vents (Humphris et al. 1995). Both show powerful, highly localized geochemical process signals in solid-phase deposits and dissolved chemical species. Both demonstrate finite lifetimes through existence of relic vent fields. Both act as focal points for biological activity (Page et al. 1991; Toulmond et al. 1994; Nelson et al. 1995), particularly in the microbial community (Cary et al. 1993; Cavanaugh 1994; Stetter 1999), with biomass significantly higher than surrounding areas and of distinct composition (Jannasch and Mottl 1985). Low hydrostatic pressure and hence lower maximum temperature, freshwater source material, and continental basement rock composition result in substantially different mineral content of emanating fluids at Yellowstone Lake, however. Biological community development is also far less complex because of the evolutionarily-short existence of the system. One of the most important differences is that Yellowstone Lake has definable, measurable inflows and outflows (compared with, for example, the eastern Pacific Ocean).

Biogeochemical reactions both form and consume reduced minerals, and as the term implies both biotic (microbiological) and abiotic (chemical) mechanisms are involved. Because the reactions have negative free energy, they may be accomplished spontaneously, often under conditions of extreme temperature, pressure, and reactant concentration, or they may be facilitated by enzymes contained within the cytoplasm of the microorganisms known for these reactions. Biogeochemical transformations and a model net reaction are given in Table 2, along with a representative microbial genus or genus prefix that biologically undertakes the transformation (cf. Brock and Madigan 1991).

Biological transformations of dissolved inorganic nutrients occur almost exclusively in the domain of microorganisms (algae, bacteria, fungi) and plants.

Table 2. Biogeochemical transformations, model net reactions, and representative microbial genus or genus prefixes.

Reductive-component model reactions	
Methanogenesis	$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$ (*Methano** spp.)
Sulfate reduction	$SO_4^{=} + 4H_2 \rightarrow S^{=} + 4H_2O$ (*Desulfo** spp.)
Iron reduction	$Fe[III] + 2e^- \rightarrow Fe[II]$ (heterotrophic respiration; e.g., *Shewanella* spp.)
Manganese reduction	$Mn[IV] + 4e^- \rightarrow Mn[II]$ (as iron above)
Oxidative-component model reactions	
Methane oxidation	$CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$ (*Methylo** spp.)
Reduced sulfur oxidations	$H_2S + \frac{1}{2}O_2 \rightarrow S^0 + H_2O$ (*Thio** spp., *Beggiatoa* spp.) $H_2S + 2O_2 \rightarrow H_2SO_4$ $2S^0 + 3O_2 + H_2O \rightarrow 2H_2SO_4$ $S_2O_3^{=} + 2O_2 + 2H^+ \rightarrow 2H_2SO_4$
Iron oxidation	$Fe(II) + \frac{1}{4}O_2 \rightarrow Fe(III) + H_2O$ (*Ferroglobulus* spp., *Gallionella* spp.)
Ammonia oxidation	$NH_3 + 1\frac{1}{2}O_2 \rightarrow HNO_2 + H_2O$ (*Nitroso** spp.)

* Denotes multiple genera in a group.

In most aquatic environments, microbial activity is restricted to photoautotrophs (photo = energy from light, auto = cellular carbon from CO_2 fixation; algae) and heterotrophs (hetero = organic matter decomposition providing both energy and cellular carbon; bacteria and fungi), with chemolithoautotrophy (chemo = energy from reduced inorganic chemicals, litho = chemicals of geologic origin, auto = CO_2 fixation; bacteria) restricted to the very bottom waters and upper few cm of sediments (Jørgensen and Fenchel 1974). In hydrothermally influenced systems, injection and mixing of relatively stable reduced geochemicals (e.g., CH_4, Fe[II], NH_4^+, H_2S, and intermediate sulfur oxidation products) provides an opportunity for accentuated chemosynthesis and population growth of bacteria responding to the available energy sources (CH_4: Distel and Cavanaugh 1994; Cheng et al. 1999; Fe: Cowen et al. 1986; Hafenbradl et al. 1996; Emerson and Moyer 1997; Mn: Mandernack and Tebo 1993; H_2: Brysch et al. 1987; Nishihara et al. 1990; H_2S: Nelson et al. 1989; Hallberg and Lindstrom 1994). Lithotrophic bacteria require the same inorganic nutrients for biomass production as photoautotrophs and many heterotrophs, and hence compete with them in nutrient cycling. The elemental stoichiometries (mol:mol) of tissue are approximately the same in all these microbes, i.e., $C_{106}\ N_{16}P_1\ S_{0.5}$.

Bacterial growth and metabolism occurs in proportion to the amount of usable nutrients in the environment, while the presence of bacteria depends upon previous access to nutrients. In the context of this work, both the presence and activity of specific bacterial types (e.g., nitrifiers, sulfur oxidizers, methane oxidizers) indicate that the respective nutrient substances are available. By utilizing an appropriate suite of metabolic measurements coupled with enumeration of specific bacterial populations, an independent confirmation of hydrothermal contributions to lake geochemistry is possible, and the extent of biological transformations in geochemical cycling may be elucidated. This paper summarizes efforts to characterize microbial community function specifically in underwater hydrothermal emanations of the Greater Yellowstone Geoecosystem.

Sampling Locations and Methods

Underwater hydrothermal vents have been sampled in Yellowstone Lake for over 15 years (Marocchi et al. 2001; Remsen et al., this volume). Three areas have been repeatedly studied: the West Thumb basin; the northern basin, including Mary Bay, Steamboat Point, Storm Point, and Sedge Bay; and the deep waters just west of Stevenson Island. Suspected vent areas were identified by observations of bubbling, hot-water upwelling, shimmering water, presence of bacterial mats or apparent mineral precipitates, or inappropriately warm water at depth. Due to the limited amount of ROV dive time and weather difficulties on the lake, most effort was focused on reliable vent areas around the above-mentioned features. On occasion, surveys with the ROV delved into unexplored flanks of active regions.

Vent samples have been collected using traditional water sampling bottles over visible bubblers, by wading with hand-held sample bottles, by SCUBA diving with sample bottles and syringe arrays (Buchholz et al. 1995), and by ROV equipped with a variety of water and solid-phase sampling implements (Klump et al. 1992). For SCUBA samples, divers identified features of interest, then opened the cap of a sample bottle as close to the orifice as possible. In some cases, 60- or 140-cc syringes were filled from the emanating water. For the ROV samples, a progressively more refined mechanism has been developed over the years (Marocchi et al. 2001; Remsen et al., this volume). Initially, the submarine's claw arm held a piece of tubing leading to a peristaltic pump on the surface vessel. The inlet was placed close to a feature and pumped water collected for chemical analysis. Later, a more independent, multiple-closed-loop sampling system was deployed (Klump et al. 1988), yielding more and deeper samples, but of limited volume (a few mL). Subsequently, larger samples were collected using multiple-syringe arrays. Syringes imparted the additional benefit of reducing sample contamination with atmospheric gases and lake water. As a result, measurement of more difficult analytes (e.g., reduced iron, hydrogen sulfide, methane, etc.) could be undertaken. Prior to each day's sampling, the entire sipper system was flushed with ultra-pure deionized water; residual dead-volume was about 30 mL. In a 8 x 140-mL sample this represented only 2–3% dilution, not intolerable for most geochemical analyses or even biological rate measurements, but somewhat more problematic for redox-sensitive analytes (iron and sulfur compounds in particular) and pure culture isolations.

On board the surface vessel, the National Park Service *R/V Cutthroat*, subsamples for sensitive analytes (dissolved gases, sulfur compounds, reduced metals, biological rate parameters, etc.) were taken by syringe (60 or 140 cc) without exposure to air or any non-plastic parts. When possible, derivatization or other means of sample preservation were taken aboard the vessel.

Chemical Analyses

Principal dissolved inorganic compounds were measured by flow injection analysis (FIA; SiO_2, NO_3^-, NO_2^-); ion chromatography (IC; Cl^-, $SO_4^=$); spectroscopy ($HPO_4^=$, NH_4^+), gas chromatography (GC; CH_4), or atomic absorption spectroscopy (AAS; Ca^{++}, Mg^{++}, Na^+, K^+, Fe, Mn) according to standard methods (APHA 1992). Iron was also determined by the ferrozine spectrophotometric method of Stookey (1970) with (total Fe) and without (Fe^{++}) reductant extraction. Total CO_2 was analyzed by the Teflon-membrane FIA method of Hall and Aller (1992). Beginning in 1997, reduced sulfur compounds (H_2S, $S_2O_3^=$, $SO_3^=$) were quantified by a scaled-up modification of the micro-bore high-performance liquid chromatographic (HPLC) method of Vairavamurthy and Mopper (1990) using dithio-bis-nitropyridine (DTNP) derivatization. Much of the analytical equipment was transported to the park, and all labile species were analyzed on site, usually within one day of sampling and preparative stabilization.

Biological Measurements

Bacterial isolates were obtained from vent water samples by enrichment, dilution, and growth on liquid or solidified media using inorganic nutrient supplements (CH_4, Fe[II], H_2S, $S_2O_3^=$, polysulfide) according to a variety of standard approaches. Enrichment and growth were accomplished at three temperature ranges reflecting types of bacteria expected in these geochemically and geothermally altered habitats (cf. Henry et al. 1994). Mesophiles (bacteria growing at temperatures lower than 40°C) were cultured at room temperature (18–25°C), while thermophiles (best growth at 60–70°C) and extreme or hyperthermophiles (growth at 80–110°C) were incubated in ovens at elevated temperatures (50°C and 80°C respectively).

Reduced sulfur-oxidizing bacteria were a particular focus of attention for several reasons: (1) Yellowstone National Park vents and geysers include representatives unmistakably rich in reduced sulfur, especially hydrogen sulfide (which is odorous) and elemental sulfur (which exhibits a halo of yellow, and sometimes crystalline precipitate, around orifices). The sulfur provides an energy source for chemolithotrophic bacteria to fix carbon dioxide as the principal building-block of tissue. (2) Sulfur-oxidizing bacteria are well represented in, or even dominate, marine hydrothermal vent systems with characteristics comparable to the vents of Yellowstone. (3) Many of the thermophilic and extremely thermophilic bacteria (i.e., growth at very high temperature) described from marine hydrothermal systems are sulfur oxidizers. (4) Certain metabolic characteristics, particularly carbon dioxide fixation in the dark, make possible an assessment of chemolithotrophic growth, including that of sulfur oxidizers, in the presence of other more common heterotrophic (organic matter-degrading) bacteria.

Chemolithotrophic activity (dark) and photosynthetic activity (light) were both assessed by an incubation method in which acid-volatile ^{14}C-bicarbonate was biologically converted into acid-stable organic-^{14}C (CO_2 fixation). All rate measurements were made in acid-washed 20-mL liquid scintillation vials using a temperature-controlled block, with ^{14}C-bicarbonate (ICN Corporation, Costa Mesa, California) added to 1 µCi/mL final activity. Dark fixation incubations extended for 9–12 hours, while photosynthesis measurements used 1.5–3 hour incubations in a light gradient (Back et al. 1991). Supplements and inhibitors were added at 1:100 or higher dilution to minimize inoculation artifacts. Incubation was terminated by addition of 2N H_2SO_4 to pH <2; capped vials were purged of unincorporated ^{14}C at the senior author's home institution in Milwaukee by shaking for 12–24 hours in a fume hood. Liquid scintillation cocktail (Hydrofluor; National Diagnostics, Manville, New Jersey) was added and samples counted in a Packard 1500 liquid scintillation counter (Packard Instruments, Meriden, Connecticut) for 20 minutes or 1% error, whichever came first. Zero time blanks were <200 DPM from additions of 2 x 10^7 DPM at inoculation. Rate calculations took into account the concentration of total CO_2 measured on site, with controls assayed in triplicate to quintuplicate depending on availability of sample and desired treatment matrix. Areal photosynthesis was modeled with the programs of Fee (1990).

Results and Discussion

Geochemical characteristics of hydrothermal fluids. Several products of hot water–rock interaction have been reliably enhanced in both marine and freshwater vents (Table 1). Comparing mid-Atlantic deep water and TAG hydrothermal vent fluids, Humphris and McCollom (1998) listed key geochemicals influenced by hydrothermal processes. Reliable increases have been documented for temperature, acidity, hydrogen sulfide, silicate, manganese, and iron (Table 1) in most marine vents, and Yellowstone Lake vents adhere to these same characteristics when compared with Yellowstone River inlet waters. On the removal side, marine systems completely remove magnesium and sulfate from their source waters, deep in the geothermal system, while this characteristic is muted in Yellowstone Lake vents (Table 1). One complicating factor is that the source concentrations of these components were small at Yellowstone, making such decreases difficult to demonstrate if they indeed occur. More significantly, it is apparent from many analyses that hydrothermal vent fluids at Yellowstone were diluted with lake water deeper in the conduits than we have been able to sample, at least in recent years. Comparison of current findings with much earlier data from Yellowstone Lake (Klump et al. 1988) suggests that vent geochemistry may have changed significantly over a decade. Because vent sites had not been marked until 2001, it is difficult to quantitatively compare among years, except on the broad scale of basin regions (e.g., Mary Bay, West Thumb) and observed extreme values. From the perspective of microbiology, however, geochemical processes were found to increase concentrations of reduced geochemicals supportive of chemosynthetic bacterial productivity in both marine and freshwater hydrothermal systems.

Dark carbon dioxide fixation—measurements of bacterial chemosynthesis. Extensive chemolithotrophic activity by bacteria in Yellowstone Lake was supported by utilization of geochemically reduced compounds and detected via dark $^{14}CO_2$ fixation in water, vent, and microbial mat slurry samples. In addition to outright chemosynthesis under favorable conditions, potential chemosynthesis was sought with the aid of incubation supplements, and microbial activity was verified through the use of specific metabolic inhibitors. In general there were three response patterns to the measurement matrix.

Active bacterial productivity using mineral-derived energy was demonstrated in many vent-orifice samples from the northern and north-central domains. The 1997 experimental design is exemplified by an active vent at Steamboat Point (Figure 2). Unamended control rates of dark CO_2 fixation were often 10–100 times higher than those of samples taken from the open lake and showed substantial inhibition by the prokaryotic protein synthesis inhibitor chloramphenicol (CAP). Methanol (MeOH) used to dissolve CAP had no effect. Addition of ammonium did not enhance chemosynthesis either by stimulating ammonia-oxidizing bacteria or by relieving possible nitrogen limitation of growth during the 9- to 12-hour incubations. Thiosulfate, a model reduced sulfur compound known to support growth of many sulfur-oxidizing bacteria, yielded a 60% stimulation of activity in this case (vent $[H_2S] = 34\ \mu M$) in the presence or absence of added ammonium. Stimulation also was eliminated by CAP, again indicating bacterial involvement. Collectively these data documented substantial bacterially mediated carbon dioxide fixation in habitats containing utilizable concentrations of

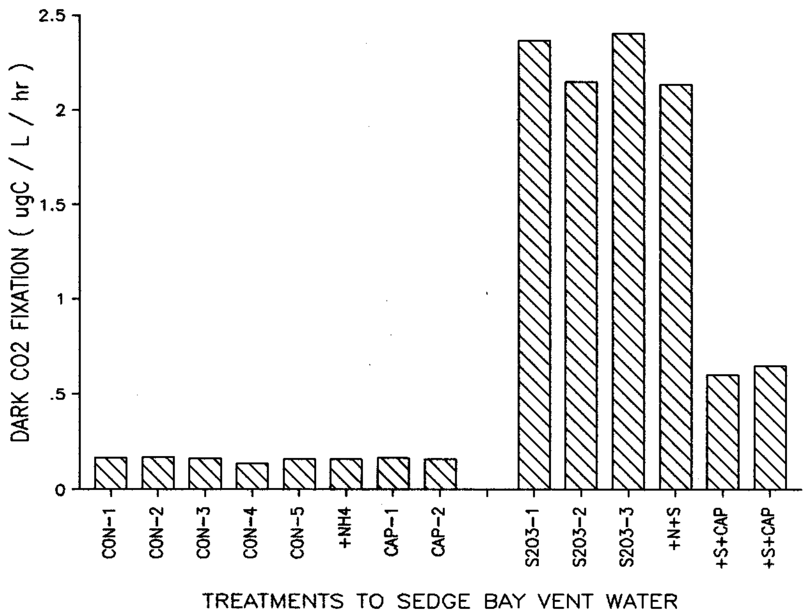

Figure 2. Response of 1998 Sedge Bay shallow-vent dark $^{14}CO_2$ fixation to added potential stimulants (e.g., 5 mM thiosulfate, S_2O_3= or S; 1 mM ammonium, NH_4+ or N; and a protein synthesis inhibitor (20 µg/mL chloramphenicol, CAP) alone or in combination (final concentration given). Individual replicates are shown.

reduced geochemicals.

Potential chemosynthesis was frequently encountered in the immediate vicinity of active vents and fumaroles, particularly where vigorous turbulent mixing of the water column was common (e.g., shallow nearshore areas) or where vent fluids were injected into confined volumes (e.g., narrow canyons). This response is well documented by a SCUBA-collected sample from a shallow (3 m deep) fissure in Sedge Bay, shimmering with warm water but readily exchangeable with overlying lake water (Figure 3). Controls and nitrogenous supplements yielded rates only 3–4 times higher than values in water taken from the open lake, but thiosulfate addition increased CO_2 fixation by over fifteenfold to levels competitive with photosynthesis. Thiosulfate stimulation was greatly reduced by CAP, as before, but the inhibitor had little effect on control activity. Often when dark fixation was low, the growth-oriented inhibitor CAP had little influence, but growth response to stimulation remained sensitive. Again ammonium addition was without effect. In these circumstances it was clear that when reduced geochemicals became available, bacterial populations were present and capable of immediate growth resumption. The spatial distribution of potential production most likely reflected the recent history and magnitude of reduced geochemical emanations.

The third type of finding was the absence of chemosynthetic activity (Figure 4), which is normal in non-geothermally influenced waters but provides an

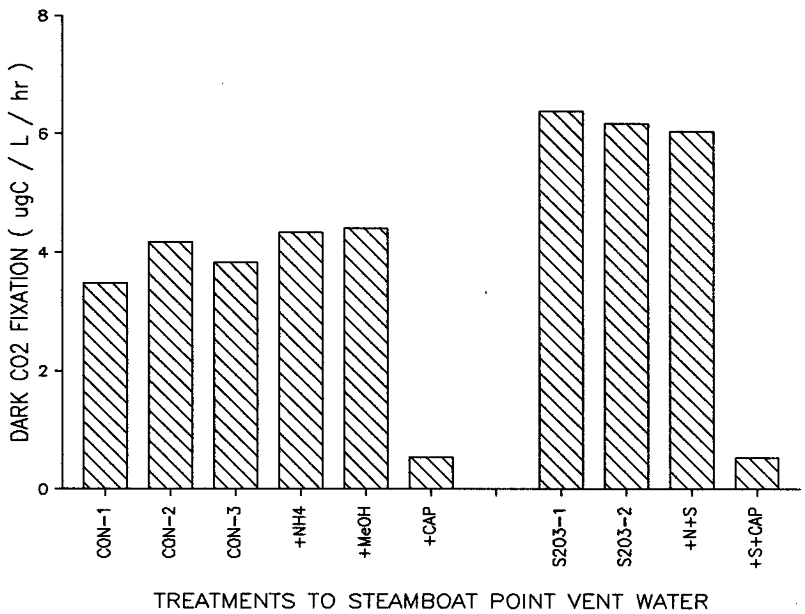

Figure 3. Response of 1998 Steamboat Point shallow-vent dark $^{14}CO_2$ fixation to added potential stimulants, as in Figure 2. Control for CAP addition was methanol (MeOH), the solvent. Due to limited sample availability, all samples did not receive all treatments.

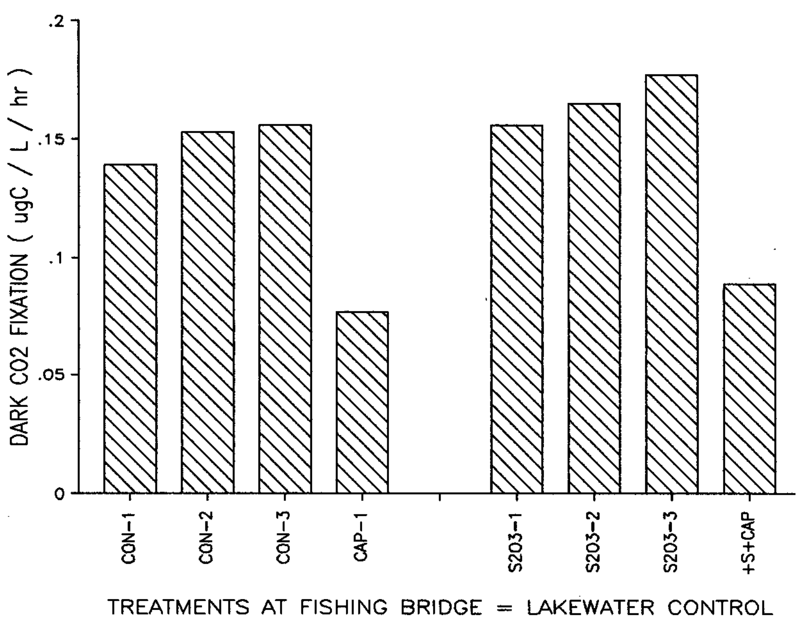

Figure 4. Response of 1998 surface water of the Yellowstone River outflow at Fishing Bridge dark $^{14}CO_2$ fixation to added potential stimulants, as in Figure 2.

important control in Yellowstone Lake. In this example, using the Yellowstone River outflow during 1997, unamended controls showed very low rates of dark CO_2 fixation (note scale expansion relative to Figures 2 and 3). Furthermore, addition of thiosulfate was not stimulatory and CAP exerted only moderate inhibition. While the absolute rates vary from extreme lows in the Southeast Arm to slightly higher values in the surface waters of the northern basin, the characteristics of non-stimulation by reduced sulfur and weak CAP effect are consistently demonstrable.

With the advent of large-volume ROV sampling (approximately 1 liter per sample) in 1997 came opportunities to measure bacterial productivity rates as well as aqueous chemistry on vent samples. Previously, only samples collected by divers or in the proximity of vents (with manual water samplers) could be tested for chemosynthesis processes to complement enrichment, isolation, and pure culture work. The 200 mL or more required for worthwhile rate measurement effort was simply too dear given the great value of interannual chemical analysis comparisons. Of the hundred samples from vents, fumaroles, water column profiles, and other lake sites, the vast majority fit one of the three above response styles. We now apply these results to understanding biogeochemical interaction of microorganisms and reduced compound emanations in specific vent fields and overlying waters.

Photosynthesis—the basis for comparison. In lakes, primary production (i.e., CO_2 fixation into organic matter) is usually carried out by photosynthetic organisms (algae, rooted plants) using light energy, in contrast to chemosynthetic CO_2 fixation described above and below. To place the bacterial contribution in perspective, a survey of photosynthesis was undertaken each year. A vertical profile of CO_2 fixation vs. irradiance was obtained with a photosynthetron (Lewis and Smith 1983) and areal productivity (mgC/m^2/day) calculated using the programs of Fee (1990). Both volumetric potential (µgC/L/hour) and most probable areal rates are relevant for comparison. Annual surveys exemplified by 1996 results provided representative photosynthesis rate ranges (Figure 5) for the main regions of Yellowstone Lake. In this approach, the light dependence of photosynthesis was measured in a light gradient, and the results used in conjunction with light penetration profiles to calculate whole water column photosynthesis (mg/m^2/day). Also relevant for comparison with chemosynthesis was the maximum volumetric rate of photosynthesis (µgC/L/hour), approximated by data between 250–800 µmol photosynthetically active radiation (PAR; 400–700 nm) photons/m^2/sec (10–30% of full sunlight).

Lowest volumetric photosynthesis was always found in the Yellowstone River inlet at the tip of Southeast Arm, with similarly low rates in the open waters of Stevenson Island and Mary Bay (1–2 µgC/L/hr). Intermediate volumetric productivity was attained in enclosed basins of West Thumb and the central Southeast Arm (3–4 µgC/L/hr), while the highest rate was found in the Yellowstone River outlet (5 µgC/L/hr). Chemosynthesis was certainly on a par with photosynthesis in the above examples, demonstrating that chemical energy

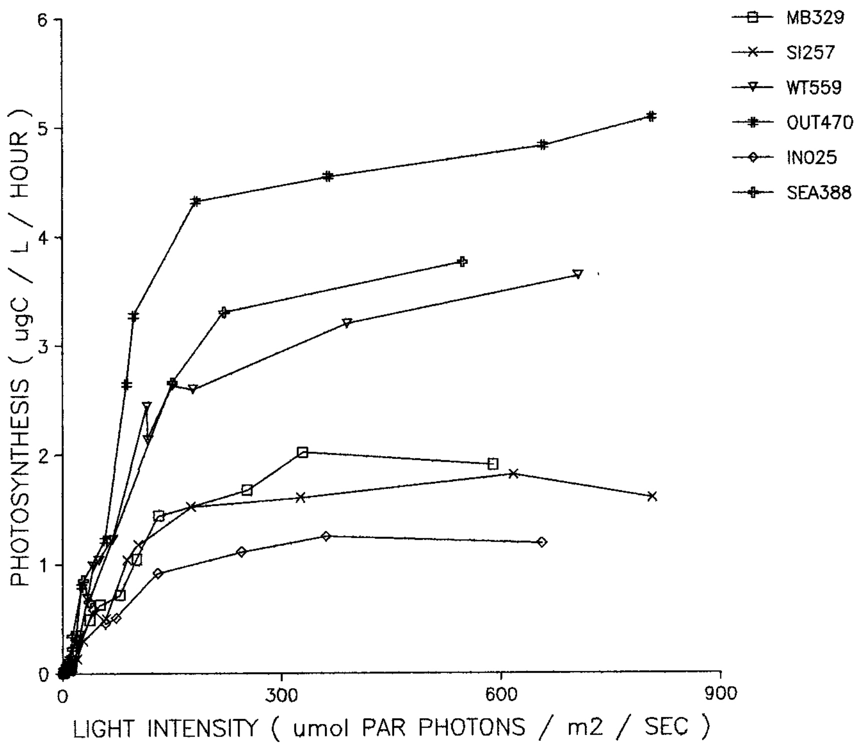

Figure 5. Light dependence of photosynthesis varied among locations in Yellowstone Lake. The three-digit number in the legend is the areal production (mgC/m2/day) calculated from these curves for 1996. MB, Mary Bay; SI, Stevenson Island; WT, West Thumb; OUT, Yellowstone River outlet at Fishing Bridge; IN, Yellowstone River inlet at Southeast Arm; SEA, Southeast Arm mid-basin.

could be as effective as light energy in promoting CO_2 assimilation into organic matter. Thus, active vents could attain sufficient production to support at least some degree of bacterial-based food web activity.

Areal production, integrated over the depth of the water column (for chemosynthesis) or over the depth of PAR light penetration (for photosynthesis), is a measure of ecosystem-level contribution. In the low-water year 1994, northern-basin chemosynthesis off Stevenson Island (3930 mgC/m^2/day) was significantly greater than photosynthesis (1620 mgC/m^2/day). Dark CO_2 fixation rates were only 2.2 µgC/L/hour but were uniform over a 75-m water column and the 24-hour day, while photosynthesis maxima were higher at 6–9 µgC/L/hour but decreased rapidly with depth (hence light) for the 14-hour light-day. Subsequent higher-water years demonstrated decreased areal photosynthesis and greatly reduced water column chemosynthesis. In the 1996 example (Figure 3), calculated areal production (mgC/m^2/day) by water column algae was highest in West Thumb (559) and Yellowstone River outflow (470) samples; intermediate in

Southeast Arm (388), Mary Bay (329), and Stevenson Island (257); and extremely low in the Yellowstone River inlet (25). Water column chemosynthesis was very low during high-water years, so areal chemosynthesis was dominated by near-vent production. At an average of 5 µgC/L/hour, vent haloes alone could account for over 100 mgC/m^2/day, a significant but limited contribution to total water column biomass production.

Biogeochemical domains of chemolithotrophy and a role for dissolved minerals. Reactions of rock and hot water at high hydrostatic pressure result in both passive geochemical leaching (e.g., chloride, silicate, carbonate) and active mineral transformation (e.g., reduction of carbon dioxide to methane, sulfate to sulfide, Fe[III] to Fe[II], Mn[IV] to Mn[II], often using hydrogen gas as reductant). In the areas of West Thumb and northern Yellowstone Lake, thermal features on shore appear to descend directly into the lake, and in fact underwater vents are abundant in those and other areas (Marocchi et al. 2001; Remsen et al., this volume). Biogeochemical domains (that is, characteristically coherent regions) appear to be important in both surface- and underwater venting systems.

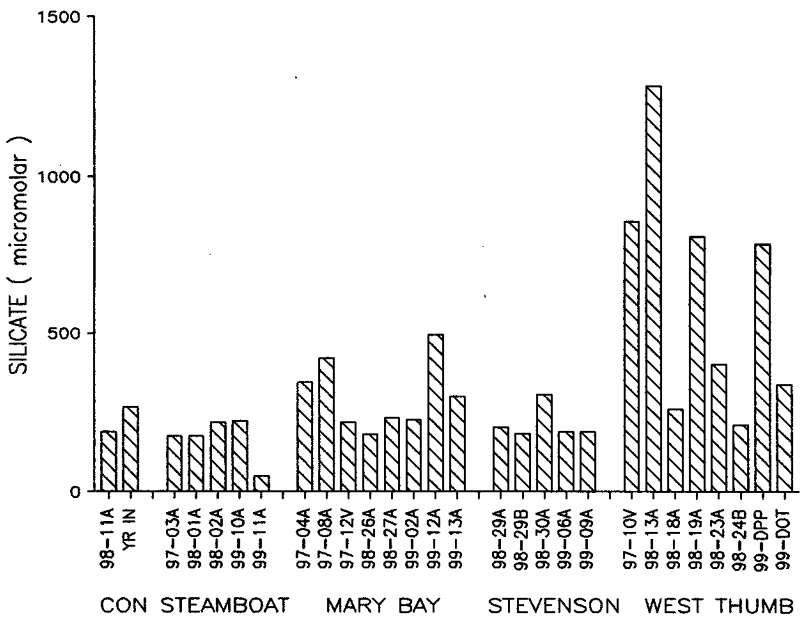

Figure 6. Domains of biogeochemistry were apparent at underwater hydrothermal vents in Yellowstone Lake, 1997–1999, as demonstrated by selected geochemical concentrations (Figures 6–10) and dark $^{14}CO_2$ fixation (Figure 11) in vent waters. Silicate showed strong enrichment in West Thumb vents. Left column, 98-11A, was a control bottom sample (35 m) taken with the ROV in a cold (10°C) inactive relic vent field in Mary Bay. YR is the Yellowstone River inlet control. From left to right, vent samples from Steamboat Point (5), Mary Bay (8), Stevenson Island (5), and West Thumb (8) are shown for each parameter. 1999 DPP (Pumice Point) and DOT (Otter vent) samples from the West Thumb area were collected by Jim Bruckner using SCUBA diving. Results are shown for all analyses, with low values appearing as blank. Missing samples (CH_4 only) have no identification label.

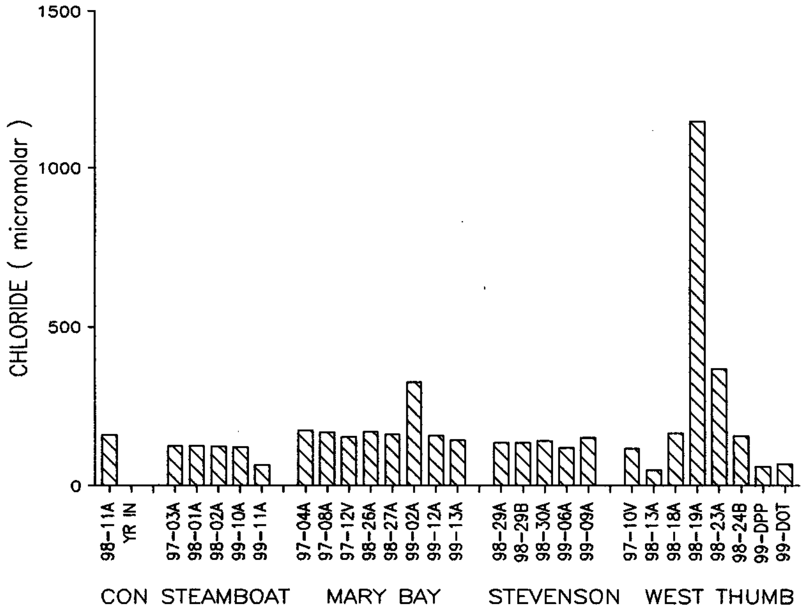

Figure 7. Chloride enrichment was less frequent in 1997–1999, but occurred in West Thumb vent waters.

Both silicate (Figure 6) and chloride (Figure 7) in hydrothermal vent fluids from West Thumb were frequently enhanced over lake water mean values of about 200 µM and 100 µM, respectively. In these and subsequent figures, vent 98-11A (far left) is a sampling control taken by the ROV sipper system very near the bottom in a deep but inactive relic vent field in Mary Bay, and represents one type of lake water control value. The Yellowstone River inlet is another important control sample. Though not all vents in West Thumb displayed elevated SiO_2 and Cl^-, only vents in this area reliably did so during 1997–1998 sampling efforts. Only slight increases in SiO_2 (less than twofold) were seen in 1997 Mary Bay and one 1998 Stevenson Island vent. The fact that only one area demonstrates high solute levels, yet all areas contain vents reaching extreme temperatures (up to 120°C), suggests that very different source reservoirs or vent conduit systems exist in the western vs. northern parts of the lake.

Three other geochemical indicators of water–rock interaction obeyed different domain specificity. Total CO_2 (lake water mean 0.6 mM) was variably but reliably enriched in all domains (Figure 8) with the most extreme values all in the Mary Bay region. Collection and handling of these samples was very important in obtaining accurate results because of degassing. Many of the vent samples formed visible bubbles with time in bottles on deck even though they were initially as warm or warmer than surface waters. For sensitive samples, however, we collected sub-samples in rubber-free syringes minutes after the submarine was out of the water. ΣCO_2 was found to decrease with a half-life of about 20 min-

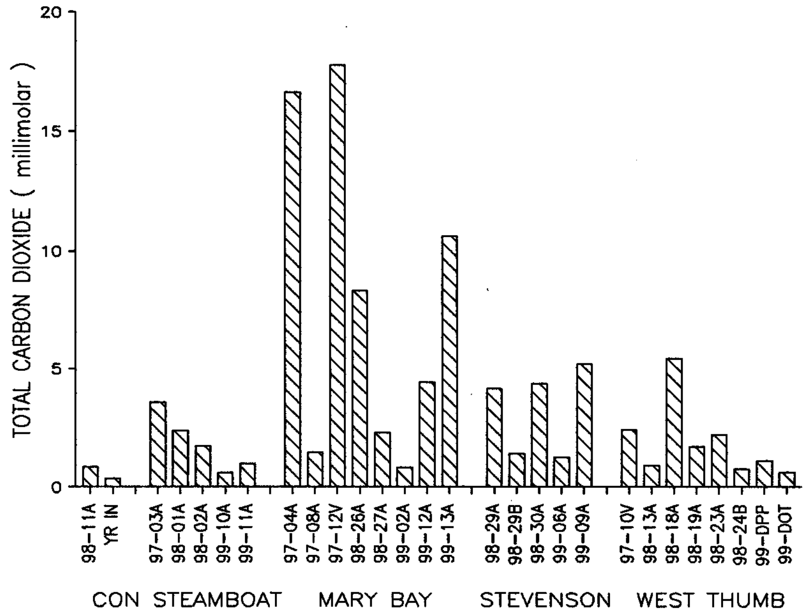

Figure 8. Total CO_2 enrichment was widespread and strong in many deeper vents regard - less of location.

utes in a beaker, but persisted undiminished for 4 to 6 hours in capped syringes (data not shown). All reported measurements of vent water ΣCO_2 were analyzed directly in capped syringes and represent the best (i.e., slightly less than to equal) estimate of *in situ* ΣCO_2. This has a strong bearing on calculations of chemosynthetic dark CO_2 fixation rates described below.

In contrast to ΣCO_2, both methane (lake water mean <1 µM; Figure 9) and hydrogen sulfide (lake water mean <0.5 µM; Figure 10) were well represented in Mary Bay and Stevenson Island vents, while they were rarely detected in West Thumb. Sulfide was also regularly found off Steamboat Point, though at a lower concentration (Figure 10). Thus, the northern and north-central domains were high in carbonate and reduced compounds, whereas the western domain did not stand out. These three components share one characteristic that differentiates them from chloride and silicate: they can exist and be transported in the gas phase. At acid pH all three are significantly or dominantly volatile, and may be distilled from reservoir fluids into a chloride- and silicate-free steam. By this mechanism the domains to the north could have origins in the same reservoir as the West Thumb vents, yet display vastly different geochemical features.

There is a strong association between the domains of reduced inorganic compound emanation and those of bacterial geochemical utilization, as exemplified by chemosynthesis measurements (Figure 11). Both extreme northern regions of the lake (Steamboat Point and Mary Bay) persistently had dark CO_2 fixation rates far above those of open lake water (approximately 0.05 µgC/L/hr) and often

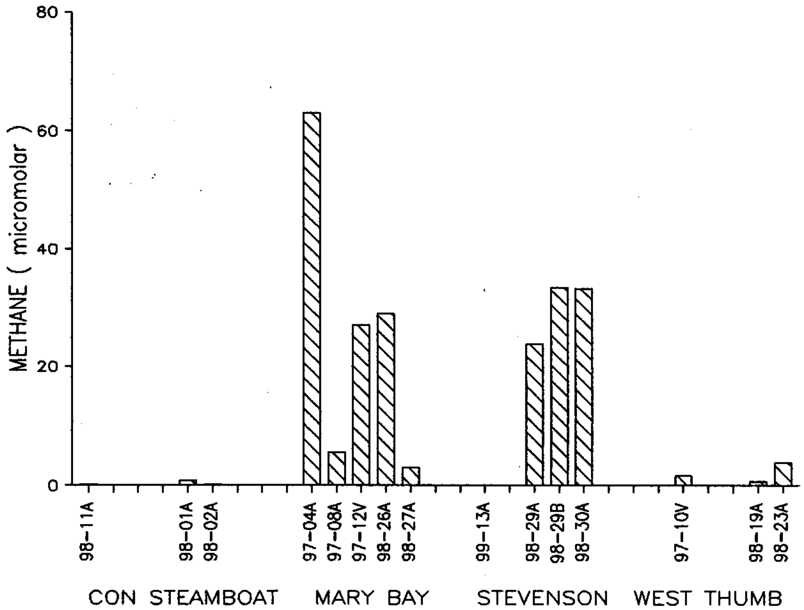

Figure 9. Methane occurred predominantly in Mary Bay and east of Stevenson Island. Analytical difficulty for this parameter in the field is apparent in missing values.

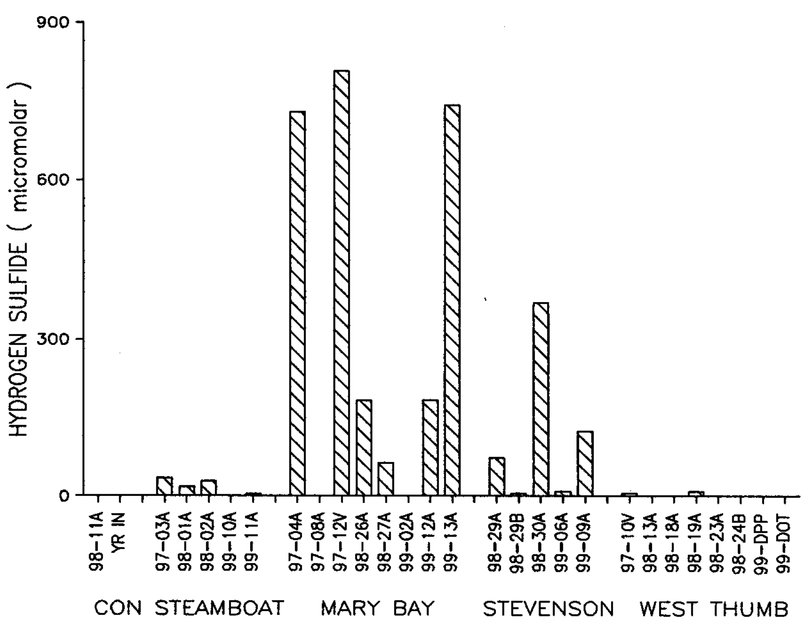

Figure 10. Hydrogen sulfide was frequently enriched in Mary Bay and east of Stevenson Island but was never of consequence in West Thumb.

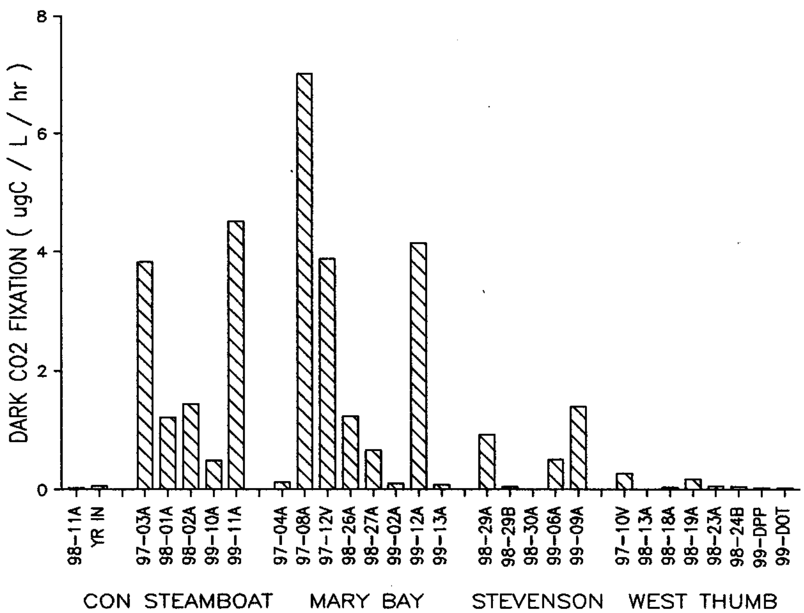

Figure 11. Bacterial chemosynthetic dark $^{14}CO_2$ fixation was common in all northern basin domains, but nearly absent in West Thumb.

exceeding photosynthesis at the surface (approximately 3 µgC/L/hr). Because CO_2-fixing bacteria require one or more reduced mineral-derived substances (e.g., H_2S, Fe[II], etc.) for growth and subsequently remove the nutrient, it is not necessary that high sulfide and high chemosynthetic rates be well correlated at a point in space and time. Hence, high levels of sulfide may presage bacterial vigor, while lower levels may be the result of consumption. In fact, in domains where H_2S was reliably present there tended to be an inverse relationship between standing concentration and bacterial productivity. However, where H_2S was rarely found, as in West Thumb, chemosynthesis was rarely found.

Temperature and microbial productivity in hydrothermal vent waters. Hydrothermal vent systems press the limits of life both through corrosive or otherwise toxic aqueous and gas phase composition, and through imposition of high temperatures. In marine habitats, sulfide and reduced iron often reach concentrations of several millimolar, with additional metals (zinc, copper, cadmium, etc.) often having concentrations in the tenths of millimolar or higher—levels rapidly fatal to most organisms of any kingdom. Toxicity of the chemical solutions is further exacerbated by vent fluid temperatures as high as 350°C in deeper, high-hydrostatic-pressure (>200 atmospheres) locations. Among the more common organisms known to humankind, thermally induced death occurs at temperatures of 42–45°C. This is a distinguishing characteristic of the mesophiles (mid-temperature-loving organisms), including virtually all plants, animals, fungi, and the overwhelming proportion of bacteria. While some organisms can survive higher temperatures, especially for short periods, the ability to thrive and grow at elevated temperatures belongs exclusively to a limited group of prokaryotic (without true organelles) bacteria and archaebacteria. These organisms, the thermophiles (heat-loving; 45–70°C) and extreme- or hyperthermophiles (70–113°C to date) are the sole inhabitants of hot, chemically inhospitable hydrothermal environments that may reflect conditions more widely distributed on early Earth or other planets (e.g., the Martian polar cap) and moons (e.g., ice-covered Europa, a moon of Jupiter). Even present-day extremophiles are restricted to the periphery of marine hydrothermal vent conduits and seeps where superheated, geochemical-laden fluids are cooled and diluted with cold ocean-bottom waters. From this perspective, Yellowstone Lake vents provide an ideal study site because the shallow depths (<150 m), resultant low hydrostatic pressure (<15 atmospheres), and in-transit mixing with lake water keep maximum vent temperatures in the vicinity of the limit currently known for growth.

Two approaches to studies of thermophily in Yellowstone Lake microbial ecology both make use of elevated temperature incubations to exclude common mesophilic bacteria for elucidation of extremophile activity. Growth, isolation, characterization, and molecular analysis of populations and strains have been a principal focus. Using growth at 50°C for thermophiles and 80°C for hyperthermophiles, enrichments and isolates for three major groups of chemolithotrophic bacteria have been successful. A thermophilic sulfate reducer has been characterized (Henry et al. 1994) and thermophilic methane- and sulfur-oxidizing bacteria have been obtained. Recently, a sulfur-oxidizing bacterium capable of growth at 80°C has also been grown. The laboratory organisms and publicly available molecular genetic database have been used as the basis for molecular probing of cultures and populations.

Presence of appropriate species of bacteria in a viable (living) state is necessary but not sufficient for expression of chemosynthetic productivity. Physical and geochemical conditions must also be supportive of growth; when they are not, bacteria may enter dormant phases that remain culturable but are actually inactive. It is partly through this mechanism that populations disperse to take advantage of either sporadic or newly established habitats (e.g., intermittent venting, opening of new geothermal features). As a first step toward corroborating molecular and culture investigations, measurements of chemosynthetic dark CO_2 fixation were sometimes paired: one at the temperature of receiving waters (4–25°C) and one at 50°C. At the elevated temperature, mesophilic bacteria are excluded, while both thermophiles and hyperthermophiles retain positive (though perhaps suboptimal in the latter case) activity in excess of their growth in bottom-water conditions.

Stimulation of chemosynthesis by 1.6–3 times during 50°C incubation was observed for three of the four vent samples tested in 1999 (Figure 12), and the fourth retained 67% of control (bottom-temperature) activity in northern and north-central basin samples. Under the same conditions, replicates of near-zero activity at 50°C were obtained at West Thumb and Southeast Arm (data not shown). Water samples sipped simultaneously from 0.5 m above the vent orifice

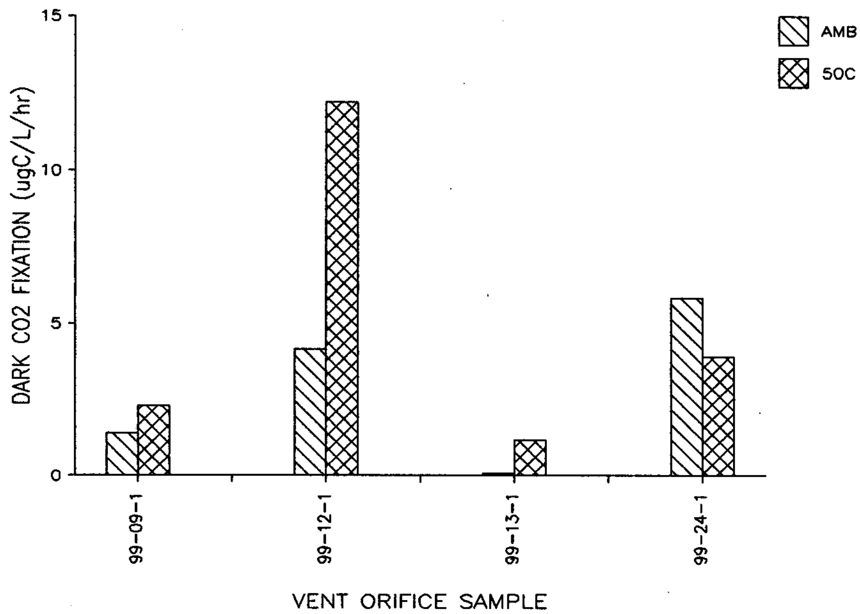

Figure 12. Elevated temperature supported or stimulated thermophilic bacterial dark $^{14}CO_2$ fixation in water samples collected within the hydrothermal vent orifice in Yellowstone Lake during 1999 sampling. Location of vents: 99-09, Stevenson Island (110 m); 99-12 and 99-13, Mary Bay Canyon (53 m); and 99-24, Pelican Roost (approximately 20 m; southeast of Mary Bay). Replicate samples (standard deviation <5%) were incubated in a temperature-controlled block at receiving water temperature (<10°C) and in an oven at 50°C.

displayed opposite behavior: more than 80% of control activity was knocked out by high-temperature incubation (Figure 13). Though measurements are few in number as yet, the method was unequivocal in selection against mesophilic bacteria. The results were consistent with growth of thermophilic bacteria within the vent conduits and their transport and expulsion into receiving waters of Yellowstone Lake. Even close to the orifice, population composition was adapted to the use of reduced mineral-derived substrates under mesophilic circumstances, leaving enrichable thermophile populations but at low proportion to total chemosynthetic bacteria. Thus, it is likely that very favorable habitats for detailed study of *in situ* living extremophile communities are present in the northern part of Yellowstone Lake. Ease of access relative to deep sea vents and a closer approximation to optimum growth conditions are significant factors when considering studies for early evolution and/or exobiological applications.

Microbial mats as persistent sources of chemolithotrophic activity. Though somewhat less tractable to quantitative analysis than vent water samples, visual evidence of microbial mats surrounding vents and fumaroles has been both ubiquitous (Marocchi et al. 2001; Remsen et al., this volume) and persistent from

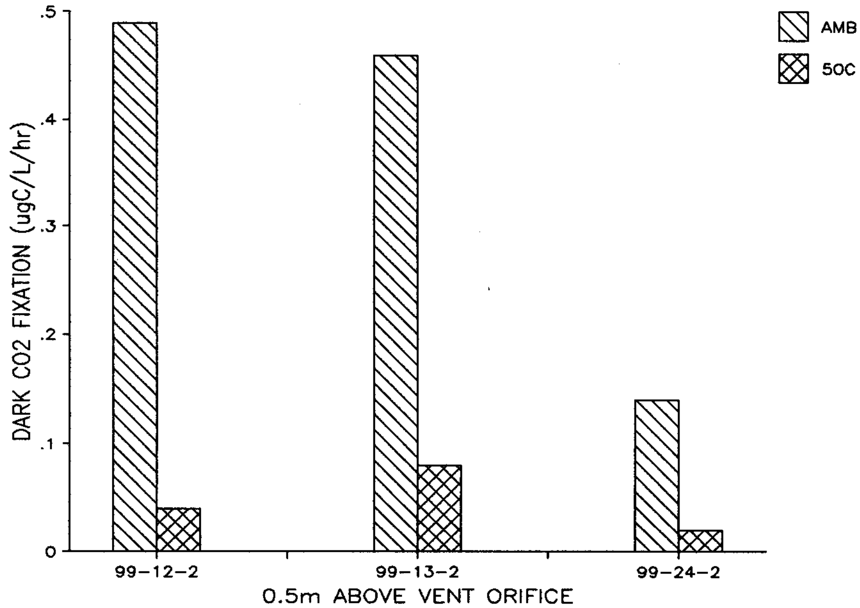

Figure 13. Elevated temperature greatly decreased bacterial dark $^{14}CO_2$ fixation in water samples collected at the top of the ROV arm, 0.5 m above the vent. Samples were incu - bated in parallel with vent orifice samples in Figure 12.

year to year. Microbial mats may be found on the sediment surface, on rock ledges overhanging vents, encrusting rooted plants in shallower water, or wherever a solid surface and dissolved mineral-laden waters come together. The very presence of entwined filaments of geochemical-oxidizing bacteria was often a clue to nearby vents and directed sampling efforts, particularly in the deeper canyons of Stevenson Island and Mary Bay. Because of their growth habit, mats could not be readily sampled with the ROV, but in 1994 SCUBA divers Lori Buccholz and Joel Kostka collected mat material in sterile Whirl-Pak bags from under an overhang of a Sedge Bay vent in late July. The mats were mildly homogenized to facilitate replicate sampling, and dark $^{14}CO_2$ uptake was measured in the presence of a variety of stimulants, primarily inorganic biomass nutrients (nitrogen, N as nitrate; and phosphorus, P as phosphate) and substrates of chemosynthesis (sulfur as thiosulfate, $S_2O_3^{=}$; nitrogen as ammonium, NH_4^+). As with some water samples, thiosulfate strongly stimulated chemosynthesis, while biomass nutrients or ammonium had no or only a minor effect on dark CO_2 fixation respectively (Figure 14). Although visible biomass was present in the samples, the rates of dark CO_2 fixation were also tenfold higher than most unamended vent water samples and were almost doubled by addition of a reduced sulfur compound, thiosulfate.

Summary: Photosynthesis and Chemosynthesis in Yellowstone Lake

The biogeochemical setting of Yellowstone Lake with its several areas of pro-

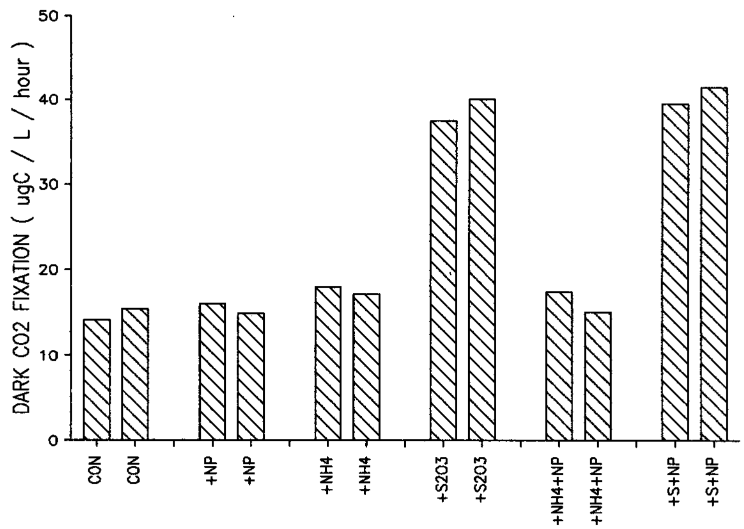

Figure 14. Vigorously chemosynthetic Sedge Bay bacterial mat slurries were stimulated further by thiosulfate addition. Supplements with inorganic growth nutrients nitrate + phosphate (+NP), ammonium (+NH_4), and combinations had little further effect.

nounced and persistent underwater hydrothermal venting provides an ideal setting for growth of mineral-oxidizing bacteria. They include representatives, many thermophilic, of the hydrogen-, reduced sulfur-, iron-, manganese-, and methane-oxidizing bacteria. Nitrifiers (ammonia oxidizers) may also be active, though few vents have been found to contain substantial concentrations of NH_4^+ in recent years. All but the methane-oxidizing bacteria assimilate carbon dioxide as the sole source of carbon for tissue. Using this assay for collective chemosynthetic activity, it was demonstrated that (1) both geochemical emanations and chemosynthetic bacterial activity were not ubiquitously distributed among Yellowstone Lake hydrothermal vents, but rather were focused in distinct regions; (2) a portion of bacteria in the vents themselves had thermophilic characteristics (enhanced or persistent production at 50°C); (3) bacteria growing in the immediate proximity of vents or in overlying waters often could be stimulated by addition of reduced sulfur compounds; and (4) slurries of white mat aggregates surrounding vents had very high rates of chemosynthetic production. Summarizing maximum rates of productivity for five years of sampling (Table 3), it was apparent that in most years vent water samples could attain rates of primary productivity (i.e., carbon dioxide assimilation into biomass) similar to that of surface photosynthesis by algae. Although access to enough vent samples for analysis of biological parameters was limited until 1997 when the syringe sampler was installed, the results still suggest that geochemical energy was sufficient to promote active, if sometimes localized, growth of bacterial populations.

Table 3. Summary of maximum rates of photo- and chemosynthesis in Yellowstone Lake, 1994–1998.

Parameter	Units	1994 Mid-July	1995 Early June	1996 Late July	1997 Mid-July	1998 Mid-July
Maximum surface photosynthesis	µgC/L/hr	6.9 ($n = 1$)	3.7 ($n = 6$)	4.8 ($n = 9$)	8.9 ($n = 4$)	4.6 ($n = 17$)
Maximum vent chemosynthesis	µgC/L/hr	3.2 ($n = 1$)	9.1 ($n = 4$)	N.D.	7.0 ($n = 5$)	1.6 ($n = 13$)
Maximum surface chemosynthesis*	µgC/L/hr	2.3 ($n = 3$)	0.11 ($n = 6$)	0.23 ($n = 7$)	0.23 ($n = 5$)	0.09 ($n = 8$)
Open water thiosulfate stimulation	% Control	50	7	2	20	4
River outflow discharge†	1000 ft^3/sec	<2	>4	>4	>5	>4

* Includes dark CO_2 fixation by algae.
† Data from United States Geological Survey Website: Gaging Station 06186500 at the Yellowstone River outflow, Fishing Bridge.

Most intriguing was the short visit in 1994, one of the two lowest-water years in the last decade (1992 being the other). During 1994, the entire basin north of Stevenson Island smelled strongly of H_2S, the beach at Mary Bay was nearly too hot to walk on, and fumarole bubbles rising through the water column off Stevenson Island broke on the surface to leave a yellow-white ring of presumed elemental sulfur from oxidation of bubble-borne H_2S. In surface samples from Mary and Sedge bays and in vertical profile at open-water Stevenson Island, dark CO_2 fixation was ten or more times that of typical dark rates for surface samples, and demonstrated strong thiosulfate stimulation. Only one vent was sampled (Sedge Bay), but it showed that under permissive conditions, chemosynthetic activity in the water column could be stimulated through physical mixing of vent-derived geochemicals to levels similar to near-vent samples. In years of high outflow, vents still provided oases of productivity capable of supporting limited animal-consumer biomass, even in deep waters where they would otherwise be absent.

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The Bridge Bay Spires: Collection and Preparation of a Scientific Specimen and Museum Piece

Russell L. Cuhel, Carmen Aguilar, Charles C. Remsen, James S. Maki, David Lovalvo, J. Val Klump, and Robert W. Paddock

Abstract

Remotely operated vehicle dives on a site of unusual depth-sounder features unveiled a field of stalagmite-like spires of possible hydrothermal origin near the Bridge Bay marina. Fragments collected from the base of several spires were composed of very low-density, porous material resembling siliceous sinter. A National Park Service dive team retrieved a 2.5-ft tall specimen in 1999, and plans for cutting and distribution were made. After a computerized axial tomography (CAT) scan revealed the interior structure, the spire was sectioned using a high-pressure water-jet saw. One half, showing both exterior and cross-sectional surfaces, was sent to the National Park Service personnel at Yellowstone National Park for display purposes. The remaining half was shared between scientists at the University of Wisconsin–Milwaukee's Center for Great Lakes Studies and the U.S. Geological Survey in Colorado. The paper documents a stepwise progression from discovery to elucidation of the spire's structure.

Introduction

Yellowstone National Park has served the public as a source of wonder, amazement, and education for more than 125 years, yet has far from exhausted its bounty of stunning scientific discoveries. While some may be of purely scientific interest, many are suitable and appropriate objects of public appreciation as well. Geological phenomena are particularly appealing in both the scientific and visitor arenas. Many such treasures lie discreetly hidden below the frequently tumultuous waters of Yellowstone Lake (Marocchi et al. 2001), and it is clear that numerous revealing features have yet to be discovered. During the last five years, an incidental observation by National Park Service (NPS) archeologists in 1996 has been systematically pursued to finally produce a specimen of probable hydrothermal origin that will provide awe and insight to scientists and visitors alike.

That Yellowstone Lake harbors intriguing hydrothermal features should come as little surprise to anyone. Walking on the West Thumb geyser basin boardwalk, for example, it is not difficult to imagine Fishing Cone as being only one of a complex of underwater bubbling pots and geysers. Likewise, smoking, malodorous beaches of Mary Bay only hint at the wealth of active vents under the surface, though vigorous bubblers are clearly visible only a few yards from shore. Nor are all of the interesting features active today; in fact, there is much to be learned from relic structures that shed light on past geological processes. However, harsh conditions of Yellowstone Lake geothermal regions have restricted access to only a few experienced and persistent groups of explorers. Active collaboration between NPS and a long-standing program of the University of Wisconsin-Milwaukee's Center for Great Lakes Studies (CGLS) and Marquette University (Milwaukee, Wisconsin) with remote operated vehicle (ROV) contractor Dave Lovalvo succeeded in bringing one of the lake's secret riches to light.

Discovery of the Spires

The story began with a team of NPS archeologists searching parks nationwide for relics of previous inhabitants. During a 1996 acoustic survey of Yellowstone Lake for submerged artifacts in nearshore areas, they ran across an unexpected series of shallow depth soundings in about 60 ft of water near the Bridge Bay marina. Alerted by these NPS scientists, the CGLS team went to the site to investigate. The Bridge Bay area had received little attention because of its apparent lack of active hydrothermal venting, but the plot from the Furuno® depth sounder (Figure 1; 10 August 1996) piqued our curiosity. A seemingly straight line of tall features jutted abruptly out of an otherwise featureless plain, much as some geysers of the Old Faithful area protrude from barren landscapes. The form was much more suggestive of accretional (building up) rather than erosional (wearing down) action, possibly during long-past geological activity. Using one of the last dive days of the season, Tony Remsen, Jim Maki, and Dave Lovalvo deployed the ROV from the NPS research vessel *Cutthroat.* Their first dive landed near enough to the structures for rapid visual investigation.

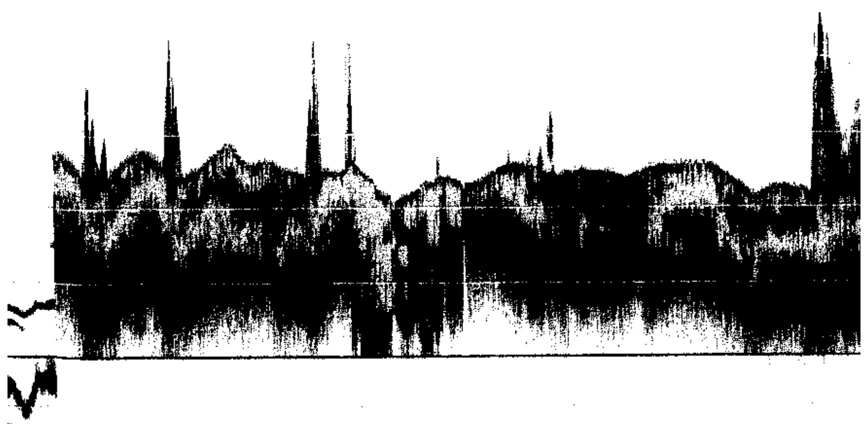

Figure 1. Bridge Bay spires are clearly visible on 1996 depth sounder charts from the R/V Cutthroat.

The visuals were stunning. Through the dim green "fog" of somewhat turbid nearshore water ghostly shapes emerged; up close, it suddenly became obvious that they were towering columns. Among the lot, graceful individual spires loomed like stalagmites (Figure 2), with clusters of spires resembling ancient

Figure 2. Backlit by green sunlight at depth, a solitary spire emerges from the turbidity at Bridge Bay in 1996. (Eastern Oceanics and CGLS)

castles interspersed among the string (Figure 3). Looming in the camera's lens, the structures varied from mere nubs to towers over 15 ft high, many covered with luxuriant growth. Well infused with natural sunlight at this depth (45–60 ft), large populations of algae covered the sides and tops. As we were to discover, a variety of animals, including colossal examples of freshwater sponges, also make the spire surfaces home (Marocchi et al. 2001). Common to the Yellowstone Lake geoecosystem, the organismal encrustation hides the true nature of the

Figure 3. Dual towers of a complex spire structure are encrusted with plant and animal growth. (Eastern Oceanics and CGLS)

underlying features. To understand what had been found, it was going to be necessary to take physical samples. The area also required some level of protection, as some evidence of damage (possibly from boat anchors, for example) was found during the initial video observation. A no-anchor zone was established by NPS, followed by negotiations to raise a piece of the spire field for scientific investigation.

Operating under a new two-year grant from the National Science Foundation (NSF) in 1998–1999, the CGLS team worked with NPS representatives to establish a procedure for obtaining and investigating a spire sample. Collecting even a small intact structure was well beyond the capabilities of the available ROV. Resource Management Coordinator Dan Reinhart agreed to arrange an expedition with Park Service divers to collect a specimen in the late summer of 1998. Due to scheduling constraints, the dive would have coincided with the last working day of the group, which would have endangered satisfactory preparation of the sample for transportation and analysis. The collection was postponed until the 1999 field season.

The spire fields and underwater vent work of the CGLS group on the NSF grant expanded to include involvement by the U.S. Geological Survey (USGS) and its associates. The USGS group, led by Drs. Lisa Morgan and W.C. "Pat" Shanks, had already done extensive mapping of Yellowstone Lake's magnetic properties. Further inspired by the Bridge Bay structures, they mounted a detailed survey of bottom topography during the summer of 1999. The first transects, in the northern basin area including Mary and Sedge Bays, led to discovery of many more, significantly larger, and extensive spire fields reaching to 100 ft tall (Elliot 2000). These observations all the more enthused the group about collecting a sample for study. The park likewise wished to obtain a display specimen for one of the visitor center's lake exhibits.

Collection of a Spire Specimen

Late in the summer of 1999 these wishes were fulfilled. On a somewhat dreary and overcast day, Dan Reinhart and Park Service divers Wes Miles (dive captain), Rick Mossman, and Gary Nelson boarded a landing-craft-like vessel captained by Dave Hall and headed out with the *R/V Cutthroat* to the Bridge Bay site. Observers from the CGLS team and USGS were also aboard both vessels. Once the features were located by sonar, the divers donned their cold-water gear (Figure 4), slid delicately off the bow into the water, checked their underwater cameras, and descended into the murky deep. From above, we could follow their progress by the trail of bubbles. Twice they surfaced, once with bags of water collected next to the base of a spire, and once bringing small pieces of "spire rubble" from scraps possibly damaged by previous anchoring. The spongy, porous, fragile fragments aroused substantial excitement: these were not at all like the hard pipes we had so often collected with the submersible! Clearly different mechanisms had been involved in the creation of these spires.

Somewhat more disappointing words then came from the divers: the small intact spire they wanted to collect was firmly rooted in the muck and couldn't be

Figure 4. NPS divers (L–R) Rick Mossman, Gary Nelson, and Wes Miles discuss sampling plans at the Bridge Bay site. (Russell Cuhel)

budged. One more try, please! Rob Paddock quickly fashioned a rope sling that would provide support for the probably very delicate sample—if it could be freed from its ancient home. After a seeming eternity, the large air bubbles at the surface were pushed apart by first a gloved hand and then a rubber-encased head, with thumbs up. The divers and boat crew struggled to lift the catch of the day out of the water and into a bubble-wrap-lined cooler (Figure 5). Much like pulling a tooth, the divers had rocked the 2.5-ft mini-spire until it broke loose

Figure 5. In a cooler on board, the intact 2.5-ft specimen exhibits a white zone of attach - ment to an adjacent structure near the base. (Russell Cuhel)

from confinement. The site of adjoinment to other structures, well below the sediment–water line, was evident as an exceptionally white spongy area on one side (Figure 5). What a find! The divers had a right to gloat over their day's work. Everyone present, including scientists from CGLS, Marquette University, USGS, and NPS, were anxious to examine the collection, but a rocking boat was certainly not the place to do it!

The spire was unwrapped on a desk at the Lake ranger station. Maki and Carmen Aguilar picked at the nooks and crannies for leeches, worms, sponges, and samples for bacterial analysis. Shanks, Morgan, and J. Val Klump prodded chips and fragments, looking at the intriguing layered structure of the apparently siliceous (glass-like) form. All marveled at the complicated swirls of mineral deposition visible on the exterior. What mysteries would be solved, or would arise, from examining the interior? Were secrets of the origin of spires and some history of Yellowstone Lake lying only millimeters away in the center? Once again, patience was required. Even during the short evening celebration, chips dried out to amazing lightness and could be crumbled easily between the fingers. It was evident that special precautions would be necessary to ensure that everyone received an uncompromised sample for their specific uses.

The spire was obviously much stronger when saturated with water, so for transport by truck to Milwaukee the intact specimen was heavily encased in bubble wrap and soaked with Bridge Bay bottom water. Upon return to CGLS, there was discouraging news from NSF: the renewal proposal for work in Yellowstone Lake had not been funded. While this did not dampen the enthusiasm for working up the year's collections, it did require a dedicated effort to secure support for further research. During 2000, the spire waited in a walk-in refrigerator while proposal-writing took precedence. At last we obtained three more years' worth of support through NSF's Life in Extreme Environments program. Also during 2000, Morgan and Shanks garnered funding from USGS and NPS to continue their high-resolution mapping of the lake bottom and magnetic anomalies. During the summer they surveyed the area between West Thumb and Bridge Bay, as well as the deep canyons east of Stevenson Island. The impetus was still strong for analysis of the spire, but how should the very fragile piece be handled? It was still completely unknown what the interior structure might be.

Preparatory Investigations

Is there a doctor in the house? By chance, Jim Maki's wife, Kay Eileen, is a doctor with St. Luke's Hospital in Racine, Wisconsin, and they came up with the idea of running a non-destructive CAT scan (computerized axial tomography; a method using X-rays to analyze density) on "our baby." The anxious "parents"—Maki, Remsen, and Klump—waited in the control room as the intact specimen was probed at 5-mm intervals. Almost 150 images were obtained, providing a detailed picture of the interior-density structure upon which we would base our sectioning. One such view, taken just above the sediment–water interface portion, is shown in Figure 6. In this rendering, dense areas are darker, while soft, porous material is lighter. The location of the section is shown as a line about

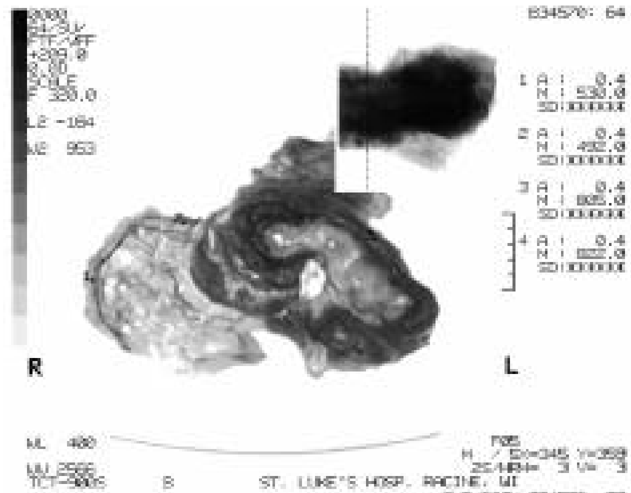

Figure 6. An X-ray cross-section of the spire at about one-third of the length from the base (vertical line on inset) reveals spongy, low-density (lighter shades) sinter in the bulb to the left side. The adjoining main spire section shows rings of higher-density material (darker shades) surrounding sinter with possible pores or conduits (white). (St. Luke's Hospital, Racine, Wisconsin)

one-quarter of the way up from the base (upper right). In the main image, the left-hand, lighter bulb is the white area in Figure 5 above, and extends to only about one-third of the height of the main spire component. The exposed edge of this section was very low-density, exceptionally white sinter with thin layers of hard, white crust meandering throughout. This portion appears almost to exude off the side of the main spire to the right. The main segment had a substantially denser external structure (dark oval), with several nearly white circular features that might have indicated vertical conduits within the column. These possible tubes did not continue to the point of the spire; rather, they became smaller and finally vanished about half-way from the bottom.

Collectively, the images provided a pre-cutting, cross-sectional map of the interior, and we opted to make four cuts to provide (1) one-half of the spire with cross-section for NPS to display; (2) one-quarter for the U.S. Geological Survey for their mineralogical analyses; and (3) one-quarter for the CGLS research team. The question now was, how? It was indisputable that the material was extremely fragile. Several concerns included the use of cutting oils, binding of the spire while moving across a cutting table, and possible fracturing of the material from the stress of cutting. Because it appeared to be primarily composed of silica (glass-like material), we consulted George Jacobson, a glass artist at Les'Glass in New Berlin, Wisconsin. Jacobson had just produced a fabulous etched rendition of a deep-sea hydrothermal vent scene on glass shower doors for us, and he was world-renowned for his leaded glass panels and other forms of plate glass work. Given the pictures of the specimen and the goals we had set, he instantly recommended Scott Cole, customer service representative of a water-jet saw facility at KLH Industries in Germantown, Wisconsin.

During our initial visit, Scott described the advantages of the water-jet saw for our application. It consists of a fine-orifice nozzle (3/64-in) through which a mixture of high-pressure water (55,000 lbs per in^2) and finely ground garnet is directed at the subject material from close range. Powerful enough to do filigree work in stainless steel while leaving satin-smooth edges, the instrument has several major benefits. First, there is no blade to bind on the work. The water jet cannot snag on regions of suddenly changing composition. Second, the nozzle is moved over the work, rather than pushing the work through the cutting edge. Third, the composition of the cutting material (water) and the abrasive (garnet) are chemically pure compared with that of machine cutting oils, and can be readily analyzed. The water is not recirculated, so the material is not in contact with waste from previous jobs. Fourth, the material need not rest on a hard surface. The tool cuts into a large water bath with wood slats across it. The work may be placed on the wood, on foam or any softer material, or on a bed of tissue: the saw will cut through that as well. A disadvantage for us is that in thick material, the physical broadening of the stream with distance means some loss of material at the bottom of the cut. Watching a current job with stainless steel, we were convinced that a test with some of the larger fragments was in order.

The first test piece was a nodule about 3 inches thick. Although it was somewhat more dense than the spire itself, the hard mineral component seemed to have the greatest degree of difficulty. This kind of material was apparently well represented around the outer crust of the spire, based on the acoustic scans. Jet saw technician Brian Bagget helped us nestle the fragment into a foam bedding on the cutting pond, after which we discussed set-up. Normally the jet saw is fully automated. A design is read into a computer aided design (CAD) file in the computer, registration points are identified on the work, the height above surface is set, and the program runs the nozzle through the x–y coordinates of the design much like a plotter on paper. For our job, the cut itself was to be linear, and it was the height above base, to follow the contours of the spire surface, that had to be varied. With more than nine years of jet saw operational experience, Bagget felt that manual control of the z-axis (height of the nozzle) during a constant-rate, straight-line run would work best. He would be able to keep the nozzle close to the surface, minimizing stream broadening, without having to make a large number of thickness measurements with subsequent programming. His effort with the fragment proved his expertise. A very flat cross-section was obtained that preserved both the detail of interior pits and pockets, and maintained intact areas near the upper edge where fractures left thin brittle plates of mineral. A second piece of smaller size but representing the silica sinter (light, porous material) also cut very cleanly and without any “shivering” that might have obliterated delicate interior features. The demonstration was convincing that this was the method of choice. An appointment for an estimated three-hour session with the actual spire was made, and we took samples of the water and the garnet abrasive for analysis.

Sectioning of the Spire for Science and the Public

To expose the interior of the sample to best advantage while retaining an undisturbed external segment for each sample, the plan was to cut across the rough bottom, or "root," to provide a flat base and cross-sectional view. Then the low-density silica "bulb" on the side would be removed. A subsequent longitudinal section would provide a full-length half-spire for the NPS museum piece, and lengthwise cutting of the remaining half would give USGS and the Milwaukee team each a representative section for analysis. Cole helped set up the spire on the cutting pond for bottom removal (Figure 7). Using a straight-line progression,

Figure 7. KLH representative Scott Cole (right) discusses set-up of the water-jet saw with the author prior to sectioning of the main specimen. The light–dark transition was the mud-line in situ. (Carmen Aguilar)

Bagget kept the nozzle as close as possible to the work, which was especially important at the fragile trailing edges of the cuts (Figure 8). The best support was thin plywood with a sheet of light foam packing material under the spire because the jet cut through the support with minimum backsplash.

Anxious as we were, the first cut across the base turned out beautifully. Figure 9 shows the fidelity of the CAT scan (Figure 6) to actual composition, with a very low-density silica mass (the "bulb" to the left) and the harder, apparently conduit-like structure to the right. The dark areas surrounding the orifices resemble iron sulfide precipitates, though analysis is currently in progress. The sample was rotated 90° and the low-density bulb was cut off parallel to the long axis of the specimen. Using the large flat edge for stabilization, a lengthwise axial cut was started up the center of the main spire. Slight expansion of the jet stream made a thin but decidedly V-shaped channel (Figure 10), but material loss was mostly confined to the softer silica material rather than the conduit segment of greatest interest. Bagget carefully maneuvered the nozzle close to the specimen all along

Figure 8. The water-jet saw finishes a transverse section across the bottom of the spire with the nozzle held close to the surface of the object. (Russell Cuhel)

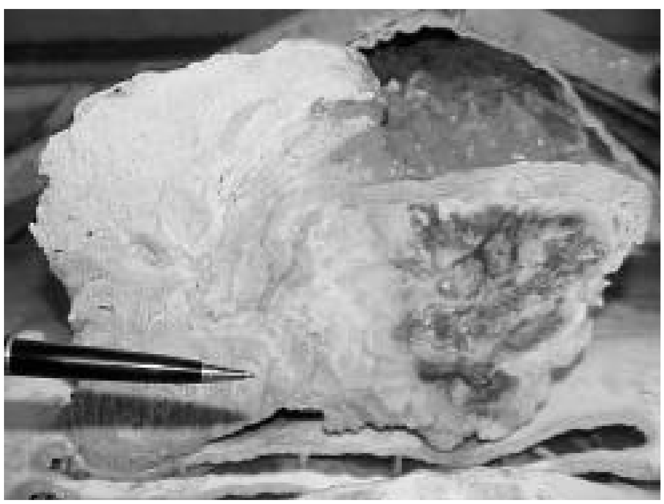

Figure 9. Cross-section of the spire viewed from the bottom reveals the porous sinter on the left and the harder main spire with dark precipitates to the right. Pen segment is 3 inches long. (Russell Cuhel)

the path (Figure 11). The water-jet saw was especially valuable at the very tip of the spire where the delicate silica was most susceptible to disintegration (Figure 12). Moving this piece through a conventional saw blade would have been a great risk to the integrity of the fine structure near the tip.

Excitement and suspense replaced anxiety as the two pieces were carefully pulled apart. Was this form the result of accretion by seepage of geothermally enriched water? Was it a product of vigorous venting through an orifice? Or was

Figure 10. Early during the axial cut along the length of the spire, stream spreading is evi - dent for the very thick base. (Russell Cuhel)

Figure 11. Technician Brian Bagget works the height adjustment to keep the nozzle as close to the specimen as possible. (Russell Cuhel)

it simply mounded into shape from adjacent sediment? The first view of the interior revealed a definitive conduit-like feature extending from the base to about one-third of the way to the tip. A thin shell of hardened material surrounded a pipe plugged with granular reddish-brown material, perfectly preserved in the sectioning. A close-up of the base region (Figure 13) shows the conduit and its contents clearly, but the feature disappeared half-way up the length of the tower. Surrounding the pipe, and accounting for most of the upper half of the spire, was more of the lower-density silica-like material. There were bands of dark precip-

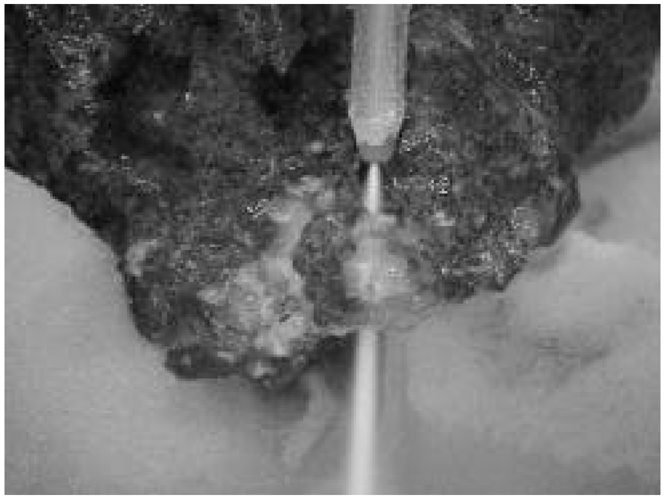

Figure 12. No sample disintegration occurred even as the cut approached the thin, delicate tip of the main spire segment. (Russell Cuhel)

Figure 13. A close-up of the presumed conduit at the base (left) of the spire shows the thin enclosure filled with heterogeneous material. (Russell Cuhel)

itate throughout the porous component, including two apparent "shells" at different distances from the exposed exterior surface. No single mechanism appeared to explain the structure; rather, it appeared as if a combination of geochemical and geophysical forces worked to shape the object. The intrigue further enhanced the value of the museum piece for NPS. In cross-section this half elegantly displays the interior structure of the spire, and, when rotated 180°, the original view of an undisturbed specimen as seen in Yellowstone Lake is retained.

The final cut would provide the material for scientific research at the U.S. Geological Survey and for the Milwaukee team. The “less beautiful” of the two halves was supported over the cutting pond and the idle nozzle run along the center of the conduit to the tip, with alignment perfected by Bagget. Starting at the base, cutting this thinner section resulted in much lower loss of material on the downstream edge of the work (Figure 14), and each now-quarter spire contained components of all of the visually apparent features for detailed investigation.

Figure 14. For the thinner half-section, stream broadening was much less pronounced during cutting even near the base. (Russell Cuhel)

Again the tool proved valuable, as the “blade” separated two sections in the very thin and fragile spire tip area.

Final Disposition of the Sections

An exploded view of the product is shown in Figure 15. A line from the sediment–water interface can be seen clearly on the forward sections. New homes of the pieces are (clockwise from center) Yellowstone National Park, Milwaukee research team, USGS, and Milwaukee team. Of the two research quarters, the one containing both the conduit and the adjoining section of silica bulb was sent to USGS scientists while the smaller quarter and disjoined bulb fragment were retained in Milwaukee. Among the many analyses underway are high-resolution electron microscopy with elemental analysis, radio- and stable isotopic age determination and geochemical formation studies, mineralogical examination, and others. Results of the combined efforts will resolve some of the mysteries surrounding the formation of the spires, as tentatively described in a *Science* “News Focus” article of mid-2001 (Krajick 2001).

Resource Considerations

Detailed scientific analysis is not necessary to recognize that the Bridge Bay

Figure 15. Spire segments arranged in exploded view as they existed in the field, empha - sizing the contrast between exterior (forward, right) and interior (rear) composition. (Russell Cuhel)

spires are both awesome and delicate. Only recently discovered, though probably thousands of years old (research in progress), it is now clear that there must be a balance struck between protection of the resource and access for public viewing. In the words of Yellowstone Center for Resources Director John Varley: “It would be the most spectacular part of the park, if you could see it” (Krajick 2001). In the lake, the spectacular views (Figure 2 and Marocchi et al. 2001) are shallow enough for sunlight to penetrate, but are accessible only by SCUBA diving. Even so, just the seemingly rugged exterior is visible, and it will be only through the park’s display that visitors can glean the complexity of the spires’ long history. With the hundreds of much larger spires later discovered by USGS in the northern end of the lake (Elliott 2000), there exist several opportunities to develop a “spire preserve.” A remaining challenge will be to provide viewing possibilities without the requirement of diving, thus increasing the breadth of public access while simultaneously protecting the features from accidental or intentional vandalism. This challenge extends beyond the spires to numerous and diverse hydrothermal geoecosystems throughout the lake (Marocchi et al. 2001; Remsen et al., this volume). For example, NPS divers or ROVs might collect a video survey of spire fields which would be played at a visitor center from CD-ROM or endless-loop video. Many other scenarios may be envisioned. For certain, the events depicted in this presentation have elevated the Bridge Bay spires from “mounds of rubble” to geological features containing some of the keys to understanding Yellowstone Lake’s past. Research in progress by all involved agencies will serve to augment the already great contribution of Yellowstone Lake to awareness of Earth’s geoecosystem functions.

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Natural Variability in Annual Maximum Water Level and Outflow of Yellowstone Lake

Phillip E. Farnes

Abstract

The water level in Yellowstone Lake varies each year in response to differences in the winter's snowpack accumulation, spring precipitation, and air temperatures. Restriction at the outlet of Yellowstone Lake retards the outflow, and water backs up in the lake during periods of high inflows. The U.S. Geological Survey started publishing Yellowstone Lake elevations in 1922 and outflows in 1926. The gage for observing the lake's elevation was originally located at the Lake Hotel dock. It was moved 1,500 feet southwest to the National Park Service dock on 17 June 1940. On 1 October 1966, the gage was moved to Bridge Bay marina, where it is currently located. The U.S. Geological Survey stopped publishing gage heights of Yellowstone Lake in 1986, but the Bridge Bay ranger staff and boating concessionaire employees have continued to make periodic water level observations. Since the early 1950s, the dates of Yellowstone Lake's freeze-up and melt-out have been obtained from ranger, resource, and marina caretaker staff. Since 1926, the highest water level recorded was 7.72 ft on the Bridge Bay staff gage in 1997. The lowest annual maximum was 2.40 ft in 1934. The 1971–2000 average annual maximum water surface elevation on the staff gage is 5.46 ft. During winter months, readings are limited, but water levels that have been recorded are usually near or below zero on the staff gage. A summary of annual maximum gage readings and outflow and dates observed from 1926 through 2001 is presented. Freeze-up and melt-out dates are available for most years since 1951. Impacts of the 1988 fires on Yellowstone Lake water surface elevations are discussed, as are methods of forecasting upcoming elevations from snow survey and precipitation data. Recommendations for future observations are presented.

Introduction

The water level in Yellowstone Lake varies in response to the winter's accumulation of snowpack within the drainage, amount of spring precipitation, and temperatures during snowmelt. The restricted outlet causes water to back up in the lake during periods of high inflow. Water surface elevations and outflow have been observed since 1922 by various entities. Observers have recorded freeze-up and melt-out dates for most years since 1951. The water level in Yellowstone Lake affects water temperatures in the Yellowstone River, spawning dates of cutthroat trout, success of spawning runs, the fishing success of bears, boating through the Bridge Bay channel, nesting success of white pelicans on Molly Islands, streamflow over the Upper and Lower Falls, downstream flows in the

Yellowstone River, shoreline erosion, and many other resources in the area. The fires of 1988 had some influence on Yellowstone Lake elevations and outflows.

Study Area

Yellowstone Lake is located in the southeastern part of Yellowstone National Park and covers an area about 136 mi^2 (352 km^2) depending on the level of water in the lake. There is no artificial regulation of lake levels. The 1,006-mi^2 (2,606-km^2) drainage area is the headwaters of the Yellowstone River, a tributary of the Missouri River. The highest point in the watershed is 12,156 ft (3,705 m) at Younts Peak in the southernmost part of the Yellowstone River headwaters. The U.S. Geological Survey (USGS) established a stream gage at the outlet of Yellowstone Lake in 1922, but only gage heights were recorded through the 1925 water-year. Outflow was measured starting in the 1926 water-year, and these data continue to be recorded and published by USGS. Elevation at the stream gage location about 450 ft (137 m) downstream from Fishing Bridge is approximately 7,730 ft (2,356 m). A separate gage for lake level observations was established at the Lake Hotel boat dock on 7 October 1921. On 17 June 1940, the lake elevation gage was moved 1,500 ft (457 m) southwest to the National Park Service (NPS) boat dock. On 1 October 1966, the gage was moved approximately 2 mi (3.2 km) southwest to the Bridge Bay marina docks. This location is about 3.7 mi (6 km) from the outlet. The datum of these gages was 7,729.51 feet from 1926–1932 and has been 7,729.45 feet since. In 1986, USGS stopped publishing the records. Gage readings have been observed since then by staff from the Bridge Bay ranger station, Yellowstone National Park resource division, and Bridge Bay marina boating concessionaire. Restriction near the outlet causes the water level in Yellowstone Lake to rise when the inflow exceeds the outflow during spring runoff. The 1961–1990 average annual precipitation for the drainage was 38.2 in (971 mm) (Farnes et al., in press) that produced an average 1961-1990 annual water-year outflow of 966,000 acre-ft (1,192 $m^3 \times 10^6$). Since 1926, this annual outflow has varied from 494,000 acre-ft (609 $m^3 \times 10^6$) in 1934 to 1,631,000 acre-ft (2,012 $m^3 \times 10^6$) in 1997. About 59% of the annual outflow occurred during the period of April through July. During the Yellowstone fires of 1988, 21% of the watershed had canopy burn. Increase in annual outflow as result of the fires was estimated to be about 3.2% (Farnes et al., in press).

Methods

Data have been obtained from USGS Water Supply Papers, the Natural Resources and Conservation Service (NRCS) database in Portland, Oregon, Yellowstone National Park archives, and from the park's resource management, ranger, and concessionaire staff. Missing records in 1983 (outflow), 1987 and 1988 (both elevation and outflow), and 1989 (elevation) have been estimated using the relationship between outflow and Yellowstone Lake elevations, outflow and downstream flows at the Corwin Springs gage, and outflow and snowpack and precipitation. In some years, the maximum outflow or staff gage readings extends for more than one day. Dates shown in Table 1 are for the latest day.

Levels from a known benchmark to the staff gage at Bridge Bay marina have probably not been run since the USGS discontinued observations in 1986. The

Table 1. Dates of freeze-up, ice-off (melt-out), maximum daily outflow, and maximum lake elevation for Yellowstone Lake, 1926–2001. Volume of maximum daily outflow is given in cubic feet per second (cfs). Annual maximum elevation given in feet, as measured on Bridge Bay staff gage.

Water-year	Date of freeze-up	Date of ice-off	Maximum daily outflow, cfs (date)	Maximum lake elevation, ft (date)
1926			3,200 (Jun 14)	3.67 (Jun 15)
1927			7,420 (Jul 01)	6.12 (Jun 30)
1928			5,680 (Jun 10)	5.25 (May 31)
1929			3,700 (Jul 05)	4.00 (Jul 02)
1930			3,780 (Jun 26)	3.95 (Jun 25)
1931			2,480 (Jun 19)	3.20 (Jun 19)
1932			5,570 (Jul 05)	5.00 (Jul 05)
1933			4,520 (Jun 30)	4.42 (Jun 30)
1934			1,740 (Jun 22)	2.40 (Jun 16)
1935			4,360 (Jul 09)	4.40 (Jul 06)
1936			4,690 (Jun 19)	4.53 (Jun 19)
1937			3,590 (Jul 01)	3.84 (Jun 28)
1938			5,950 (Jul 02)	5.32 (Jul 03)
1939			3,230 (Jul 09)	3.68 (Jul 09)
1940			3,590 (Jun 23)	4.04 (Jun 21)
1941			2,750 (Jun 28)	3.48 (Jun 27)
1942			3,890 (Jul 13)	4.41 (Jul 09)
1943			6,900 (Jul 10)	6.26 (Jul 10)
1944			3,450 (Jul 10)	4.03 (Jul 10)
1945			3,940 (Jul 17)	4.48 (Jul 20)
1946			3,700 (Jun 24)	4.20 (Jun 19)
1947			4,490 (Jul 11)	4.78 (Jul 14)
1948			5,580 (Jun 19)	5.45 (Jun 20)
1949			5,260 (Jun 23)	5.15 (Jun 23)
1950			6,120 (Jul 11)	5.76 (Jul 12)
1951		May 18	5,090 (Jul 10)	5.18 (Jul 11)
1952	Dec 26	May 16	5,340 (Jun 15)	5.25 (Jun 16)
1953	Dec 25	May 20	4,240 (Jul 06)	4.58 (Jul 07)
1954	Jan 11	May 18	5,580 (Jul 05)	5.52 (Jul 02)
1955		May 27	4,090 (Jun 30)	4.66 (Jul 01)
1956	Dec 14	May 25	7,570 (Jun 21)	6.54 (Jun 18)
1957	Dec 23	May 29	5,270 (Jul 04)	5.32 (Jul 04)
1958	Dec 31	May 21	3,500 (Jun 13)	4.24 (Jun 24)
1959		May 27	5,590 (Jun 28)	5.47 (Jun 30)
1960	Dec 18	May 22	3,210 (Jun 21)	4.05 (Jun 22)
1961	Dec 11	May 27	3,690 (Jun 20)	4.43 (Jun 22)
1962	Dec 10	May 21	5,780 (Jul 02)	5.73 (Jul 01)
1963	Jan 12	May 30	5,230 (Jun 25)	5.50 (Jun 26)
1964	Jan 08	May 29	6,420 (Jul 09)	6.06 (Jul 09)

continued

Table 1 (continued)

Water-year	Date of freeze-up	Date of ice-off	Maximum daily outflow, cfs (date)	Maximum lake elevation, ft (date)
1965		May 28	6,820 (Jul 11)	6.47 (Jul 11)
1966	Jan 16	May 21	3,570 (Jun 24)	4.64 (Jun 25)
1967		May 31	6,590 (Jul 09)	6.28 (Jul 06)
1968	Dec 15	Jun 02	4,600 (Jun 30)	5.28 (Jun 30)
1969	Dec 21	May 17	4,500 (Jun 08)	5.24 (Jun 29)
1970	Dec 28	Jun 04	6,460 (Jun 30)	6.33 (Jun 30)
1971	Dec 14	May 31	8,140 (Jun 29)	7.06 (Jun 30)
1972	Dec 28	Jun 02	6,880 (Jun 24)	6.38 (Jun 24)
1973	Dec 10	May 27	3,460 (Jul 01)	4.37 (Jul 01)
1974	Dec 24	May 27	9,120 (Jun 30)	7.34 (Jun 30)
1975	Jan 01	Jun 07	6,360 (Jul 14)	6.06 (Jul 15)
1976		May 21	5,380 (Jul 12)	5.68 (Jul 07)
1977		May 13	2,130 (Jun 20)	3.45 (Jun 22)
1978	Dec 21	May 17	5,400 (Jul 12)	5.74 (Jul 12)
1979	Dec 28	May 27	3,710 (Jul 02)	4.78 (Jul 02)
1980	Dec 29	May 10	3,770 (Jul 06)	4.78 (Jul 09)
1981	Jan 12	May 19	4,250 (Jun 28)	5.09 (Jun 29)
1982	Jan 07	May 26	7,670 (Jul 12)	7.00 (Jul 09)
1983	Dec 15	May 30	4,700 (Jul 11)	5.40 (Jul 11)
1984	Dec 22	May 31	5,080 (Jul 08)	5.74 (Jul 10)
1985	Dec 06	May 21	3,470 (Jun 19)	4.66 (Jun 25)
1986	Dec 11	Jun 04	7,360 (Jun 20)	7.01 (Jun 19)
1987	Dec 16	May 08	2,000 (Jun 16)	3.55 (Jun 16)
1988	Dec 24	May 19	2,150 (Jun 21)	3.70 (Jun 21)
1989	Dec 18	May 18	4,470 (Jun 22)	5.20 (Jun 22)
1990	Dec 30	May 20	4,290 (Jul 03)	4.95 (Jul 05)
1991	Dec 21	Jun 01	5,670 (Jun 22)	5.74 (Jun 22)
1992	Dec 17	May 08	2,780 (Jun 30)	3.94 (Jul 01)
1993	Jan 04	May 28	4,700 (Jun 23)	5.04 (Jun 24)
1994	Dec 27	May 16	3,000 (Jun 10)	3.92 (Jun 12)
1995	Dec 25	Jun 03	5,730 (Jul 13)	5.70 (Jul 13)
1996	Dec 01	Jun 03	8,730 (Jun 28)	7.08 (Jun 24)
1997	Dec 19	May 20	9,930 (Jun 19)	7.72 (Jun 22)
1998	Dec 26	May 15	4,750 (Jul 08)	5.20 (Jul 11)
1999	Jan 26	May 29	6,720 (Jun 27)	6.44 (Jun 29)
2000	Dec 28	May 06	4,250 (Jun 14)	4.94 (Jun 08)
2001	Dec 27	May 15	2,520 (Jun 14)	3.56 (Jun 16)
average, 1971-2000	Dec 24	May 23	5,200 (Jun 29)	5.46 (Jun 29)

staff gage was replaced at the same elevation and location on 25 September 1998 because ice had destroyed some numbers on the lower portion of the gage. Double-mass analysis was used to compare annual maximum outflow with the highest water levels of Yellowstone Lake and the maximum annual outflow with the annual weighted snow and precipitation values for period of record.

Results

Data for Yellowstone Lake freeze-up, melt-out, maximum annual outflow, and maximum water level are shown in Table 1 for water-years 1926 through 2001. The water-year starts on October 1 and goes through September 30. Some data were estimated, as noted above. Double-mass analysis comparisons between maximum daily outflow and staff gage readings of water surface do not show any significant breaks for the period of record. However, there are some differences associated with each individual staff gage location. Analysis using double-mass regression suggests that the annual maximum lake level since the 1988 fires may have been reduced slightly even though the total inflow volume increased. This was due to increased melt rates in the fire-generated openings in the forest canopy, which spreads the snow melt over a longer period due to the increase in percentage of open stands (McCaughey and Farnes 2001). Freeze-up and melt-out dates are functions of air temperatures and early-winter water levels in Yellowstone Lake. However, no detailed analysis has been performed to develop a relationship. Assuming low-water levels near zero on the staff gage around the time of ice-off, the spring rise in the lake water level over the past 75 years has varied from about 2.5 ft (0.7 m) to 7.75 ft (2.4 m), with an average annual rise of about 5.5 ft (1.7 m). The maximum elevations of the water surface in Yellowstone Lake and the maximum outflow from Yellowstone Lake are well correlated (R^2 = 0.927) for the entire period of record (1926–2001) for the staff gage at three locations. Separating the correlations for period of record at each gage location improves the R^2 to 0.989, 0.971, and 0.970 for the three locations.

Summary

Both the outflow and maximum water surface elevation of Yellowstone Lake for each year are functions of the winter's snow accumulation and spring precipitation inputs, and vary significantly from year to year. Yellowstone Lake's water levels and outflows have a direct effect on many of the resources in the vicinity of the lake or downstream. Water temperatures are suppressed in heavier-snowpack years as meltwater draining out of the snowpack is near 32°F (0°C). These suppressed stream and lake temperatures delay emergence of salmon flies and spawning of cutthroat trout. Success of spawning runs has been related to runoff and can influence recruitment of cutthroat trout (Farnes and Buckley 1964). Streamflows during spawning runs affect success of bears feeding on migrating and spawning cutthroat trout (Dan Reinhart, personal communication). High and low lake levels affect tour boating and boat rental operations by the Bridge Bay concessionaire (Hal Minugh, personal communication). Nesting success of white pelicans has been greatly diminished during years with high water levels because the Molly Islands are almost completely covered with water then (Terry McEneaney, personal communication). Shoreline erosion can be accelerated in high-runoff years particularly if accompanied by wind during times of the highest water levels. Downstream water users have been affected by low-water years (e.g., by shortages of in-stream flows and irrigation water supplies).

Recommendations

Since the elevations of the water surface in Yellowstone Lake affects many resources, it would be desirable to have the Montana office of the USGS Water Resources Division resume responsibilities for Yellowstone Lake level observations at the Bridge Bay gage and make these data available to the public in a manner similar to that of the outflow observations. This would provide a level of accuracy comparable with that of earlier records.

Have the Montana office of NRCS develop procedures to forecast upcoming elevations of Yellowstone Lake at the Bridge Bay gage using snow–water equivalent, soil moisture under the snowpack, and spring precipitation and make this information available on their Web page in a format similar to that of other water supply forecasts. This would provide warning of low or high water levels that could affect resources associated with lake elevation. It would also permit researchers advance time to arrange for collection of any related data that might be pertinent to their study.

Suggest that researchers consider the impacts of natural variability in inflow, lake levels, and outflow when researching phenomena associated with Yellowstone Lake.

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Rich in Resources, Short on Cash: How Philanthropy Helps Yellowstone and Other National Parks

Kézha Hatier-Riess

Introduction

The purpose of the Yellowstone Lake Conference was to encourage awareness and application of wide-ranging, high-caliber scientific work on Yellowstone Lake. The lake basin is one of Yellowstone's greatest resources and is increasingly being recognized by the scientific and conservation world for its significance. Because the full implications of the changing geology and ecology of the lake area are still unknown, the opportunities for research and discovery are many. Unfortunately, federal funding for science-related projects in national parks is insufficient to meet the growing needs of research. If studies on the relationships between the regional landscape and its resident species are delayed in Yellowstone and other national parks until federal funding is available, irreplaceable resources and information could be lost forever.

Due to a lack of human development, as well as limits on recreation, protected lands such as national parks are great laboratories for research. With the ceaseless growth of urban areas, these protected lands are becoming more important to our civilization. Yet high-quality research is often expensive and, though important, is usually not as high a priority for federal funding as are the reconstruction of roads, the reroofing of leaky buildings, or the repair of hazardous structures. Furthermore, an important part of research is the use of the results. Even if a research project is federally funded, there is often limited or no funding available to disseminate the valuable information that is discovered.

Increasingly, philanthropy is being used to help the National Park Service (NPS) protect ecosystems, improve education, fund research projects, and inform the public about the results of the significant scientific work that is happening in Yellowstone and other national parks.

The History and Current Role of Philanthropy in Protecting National Parks

The national park idea was started in the United States and has since spread throughout the world to help protect in perpetuity some of our earth's most precious lands. The donating of private money to public causes is also primarily an American phenomenon. Philanthropy played an important role in helping to establish and protect national parks and in creating the NPS. Before the NPS was established in 1916 and Congress appropriated funds each year to run parks—and later, when land acquisition needs to expand the national park system exceeded available federal appropriations—private donations were responsible for substantial additions and funding to parks.

Barry Mackintosh, a former NPS historian, lists a number of examples of the earliest philanthropic efforts in national parks in his paper "Philanthropy and the National Parks" (Mackintosh 1998). The following paragraph highlights some examples from his paper, which is an excellent summary of the role of philanthropy in national parks.

Among the earliest large donations were a 1907 land donation from Mr. and Mrs. William Kent, which allowed for the creation of Muir Woods National Monument. Another land donation came in 1916 from a group of private donors for what is now Acadia National Park. Before Stephen T. Mather became the first director of the NPS, he too gave a substantial amount of his own money for the protection and administration of national parks, including funds to buy more land for Yosemite National Park and money to publish the *National Parks Portfolio.* This portfolio was distributed to 250,000 people and was helpful in drumming up support to convince Congress to create the NPS on 25 August 1916. In the early 1900s, the Rockefellers donated a significant amount of money and land for national parks, including millions of dollars to buy land for Acadia, Grand Teton, Great Smoky Mountains, Virgin Islands, and Yosemite National Parks, among others. Since the 1940s, the Mellon family has given millions of dollars to acquire lands for the public, including for Gettysburg National Military Park and Shenandoah National Park, as well as to preserve existing parklands at Redwood and Rocky Mountain National Parks. More recently, in the 1980s individuals, foundations, and other non-profit entities donated $350 million to refurbish the Statue of Liberty and restore Ellis Island's Great Hall. The latest substantial act of philanthropy in the United States was from the Haas family, who donated $16 million to transform Crissy Field in Golden Gate National Recreation Area from a dirt wasteland into a beautiful waterfront park.

Mackintosh's paper ends with a discussion of how Congress recognized the importance of philanthropy in the protection of parks and established the National Park Foundation in 1967, which was launched, appropriately, with a $1 million donation from Laurance Rockefeller. The National Park Foundation raised more than $35 million in 2000 for the benefit of all national parks. Since the creation of the National Park Foundation, more than 20 other non-profit groups that raise money for national parks, called "friends groups," have been established to help individual parks. Yellowstone's friends group is called the Yellowstone Park Foundation.

The Current Role of Philanthropy in Protecting Yellowstone

The Yellowstone Park Foundation and other friends groups do not replace congressional funding for national parks, but enhance it. The purpose of friends groups is to help the NPS achieve a margin of excellence by funding programs that do not directly affect visitor and staff safety, but that enhance the experiences of visitors in parks and the protection of natural and cultural resources in ways that are beyond the financial capacity of the NPS.

In 2001, Yellowstone received $25,122,000 in direct federal appropriations, $5,656,000 in user entrance and special use fees, and $714,000 in concession fees—a total of $31,492,000 to run the park. This equates to approximately $10 spent on each visitor to Yellowstone to fund interpretive talks, ensure visitor safety, provide adequate staffing to meet visitor needs, clean campgrounds, and create educational exhibits—just part of the unseen work that is done for the benefit of each visitor.

Assuming an annual visitation to Yellowstone of about 3,000,000, the abovementioned work is done by a full-time staff of approximately 556 people—which means that each full-time employee is responsible for approximately 6,000 visitors per year. The level of federal funding has prevented the park from filling 15% of its permanent positions and has led to a number of operations being reduced or cut, including exotic species control, monitoring park resources, ranger patrols, and interpretive programs. Yet, all of these cut programs are essential to the long-term protection of Yellowstone's resources and to visitor fulfillment.

Though Yellowstone was not the recipient of many of these large, early donations mentioned earlier as part of Mackintosh's paper, philanthropy is now playing an increasingly important role in the conservation of and research on the world's first national park.

Much of the philanthropy that has taken place in Yellowstone has been done quietly. Therefore few people know if a research, interpretive, or wildlife restoration project has been funded with private money. But millions of private dollars have been designated for Yellowstone's benefit in recent years.

Recent philanthropic contributions to Yellowstone include close to $1,000,000 contributed by American Gramaphone and its owner, Chip Davis, to help restore the park after the 1988 wildfires. This large gift was used for trail rehabilitation projects and educating the public about the role of fire in Yellowstone's ecosystem through funding a supplement to the park newspaper. Later, American Gramaphone funded the "top ten issues" supplement to the park newspaper. The Yellowstone Association has contributed more than $6.5 million since 1933 to provide educational programs, exhibits, and publications for park visitors. The Association also runs the Yellowstone Institute, which offers a variety of courses that teach people about the ecological processes of Yellowstone. Moose Charities has long been a supporter of Yellowstone by funding the park's Youth Conservation Corps program each year for 12 years. Their donations have totaled more than $1,500,000 since 1989.

In 1996, Conoco donated $200,000 in seed money to start the Yellowstone Park Foundation. Since then the company has donated more than $2.2 million, including $2 million for a new visitor education center at Old Faithful for which the Foundation, in cooperation with NPS, is currently raising money. This new visitor education center will have a large theater and classrooms and will be an important hub for education and research on Yellowstone's geyser basins. Unilever launched the Old Faithful Visitor Education Center campaign by donating $1.25 million for the cause. They also have donated a considerable amount of recycled material for boardwalks throughout Yellowstone, including for the boardwalk that circles Old Faithful.

Defenders of Wildlife has made a considerable difference in the protection of Yellowstone's wolves and grizzly bears by providing money to ranchers for livestock lost to these predators. National Parks Conservation Association (NPCA) advocates for the protection of Yellowstone and other national parks and has recently worked with park staff to create a business plan that NPCA plans to use to encourage more financial support of national parks from Congress.

Canon, USA, and the Turner Foundation have both contributed large donations for research and education in Yellowstone. For example, starting in 1997 Canon donated a total of $300,000 over three years to fund conservation research on grizzly bears and amphibians, and for native plant and native fish restoration. The Turner Foundation has been a long-time supporter of Yellowstone, including supporting wolf restoration and research on the army cutworm moths that are one of the favorite and most important fall food sources for grizzly bears.

Why National Parks Should Not Simply Make Do with the Federal Funds that Congress Appropriates

Though the world has changed profoundly since Yellowstone was created in 1872, the role of national parks has evolved with the needs of our country and now provides benefits of fundamental importance to virtually every community in America. The future would be bleak without national parks. The programs they provide include everything from campfire talks in Yellowstone about wildlife, to discussions of the history of early civilizations at Aztec Ruins National Monument in New Mexico, to learning about civil rights at Frederick Douglass National Historic Site in Washington, D.C.—yet all of these NPS units are struggling for viability.

In December 1999, the director of the NPS asked the National Park System Advisory Board to "develop a report that should focus broadly on the purposes and prospects for the National Park System for the next 25 years." An excerpt from the resulting 2001 report, titled *Rethinking the National Parks for the 21st Century*, states the following:

> Private citizen involvement with national parks has a long history. In recent years the number of volunteer 'friends' groups supporting individual parks has grown significantly. These groups provide tens of millions of dollars each year to support individual park operations and enrich the quality of public service offerings. The work of the friends groups is extremely valuable to the Park Service…National parks will always be dependent on federal appropriations for their primary support. However, the opportunity to provide additional private resources for the parks should be encouraged. The added value expressed through private funding is a measure of the importance placed on this revered American institution (National Park System Advisory Board 2001: 29, 30).

Conclusion

Barry Mackintosh writes:

> Philanthropy is more than a source of land and money for the parks. It is a means of building and strengthening bonds between parks and their advocates.

> While all taxpayers contribute to the parks, those who make additional voluntary contributions will have a special interest in the park's welfare. The parks and the National Park Service benefit from their devotion as well as their dollars.

As our daily environment is filling with strip malls, as we watch our farmlands being replaced by parking lots, and as our world becomes more technologically and politically complicated, national parks are an increasingly important source of connecting with our roots and of peace and refuge. Their role as a laboratory and an infinite source of learning and wonder is only strengthened. Yet as parks become more essential to our world's balance, the economic and physical demands on them become greater. Without what Mackintosh mentions as the private sector's devotion to enhancing federal funding, access to national parks may have to be restricted and education programs cut even further. We may lose vital elements of the very places of solitude and wonder that we seek.

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Archeology Around Yellowstone Lake

Ann M. Johnson

In this paper, I will be looking at Yellowstone Lake during the Precontact period—that time in the past before written records—and I will summarize our current thinking about who was here and when, what their activities and subsistence practices were, and how these activities varied across the seasons. These questions are, of course, interrelated. Presentations in this symposium cover a grand diversity of topics relating in one way or another to Yellowstone Lake. Through archeology, we can learn about the people of many cultures who visited and lived here at different times in the past, and compare their different adaptations to the changing environment. The unique contribution that archeology brings is that of time depth. In addition, archeological sites also contain bits of pollen, burned seeds, animal bones, and other residue remains from which it is possible to learn about the past environment, including its plants and animals.

Before discussing what we have learned about the past, I need to first describe the data from which my thoughts and impressions are derived (Figure 1). Yellowstone Lake has 100–110 miles of shoreline and seven islands. At the pres-

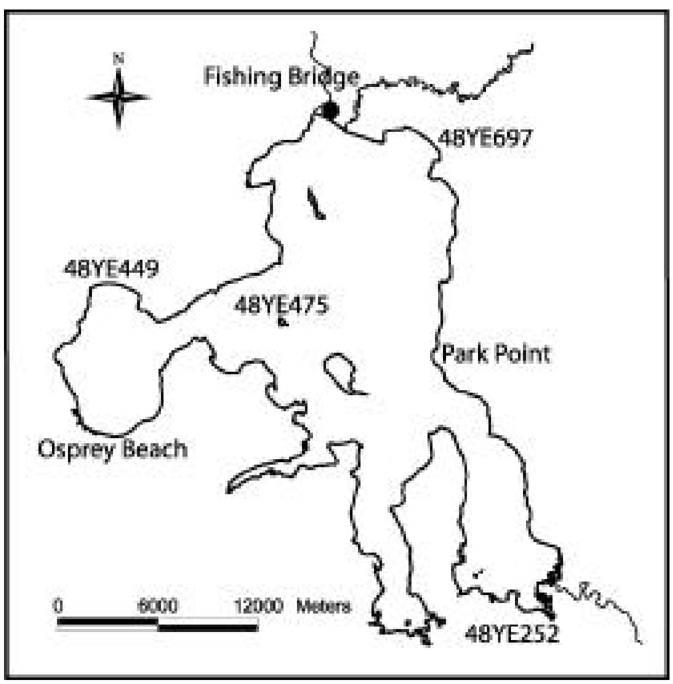

Figure 1. Archeological sites around Yellowstone Lake.

ent time, there is a good-quality archeological inventory for only about 10 miles of shoreline, with occasional reporting of sites along another 50 miles. These are primarily on the north and west sides of the lake. Additionally, there are archeological sites on six islands, but a reasonable inventory is available only for Dot and Peale islands. Most sites are known only from eroding cultural deposits or a few tools. It is ironic that our best information about prehistoric use of Yellowstone National Park comes from cultural deposits that are being destroyed by erosion.

Chronology

The most basic question is, When were people here? Figure 2 illustrates the frequency of radiocarbon dates for the entire park in 300-year increments, with the year AD 2000 on the left side. Dates in the text are in BP (years before present) starting at AD 2000. There are few dates for the oldest and the most recent human use of the park. We expect to find that all of the earliest peoples in Montana, Wyoming, and Idaho visited Yellowstone Lake. In fact, more of the points representing early (Paleoindian) use of the park are found around the lake than any other area. This is due to the greater erosion, and thus exposure of sites, in this area. But unfortunately, sites from 7,000 to 11,000 years ago are rarely identified, at least in part because they have been removed by natural erosion or are buried.

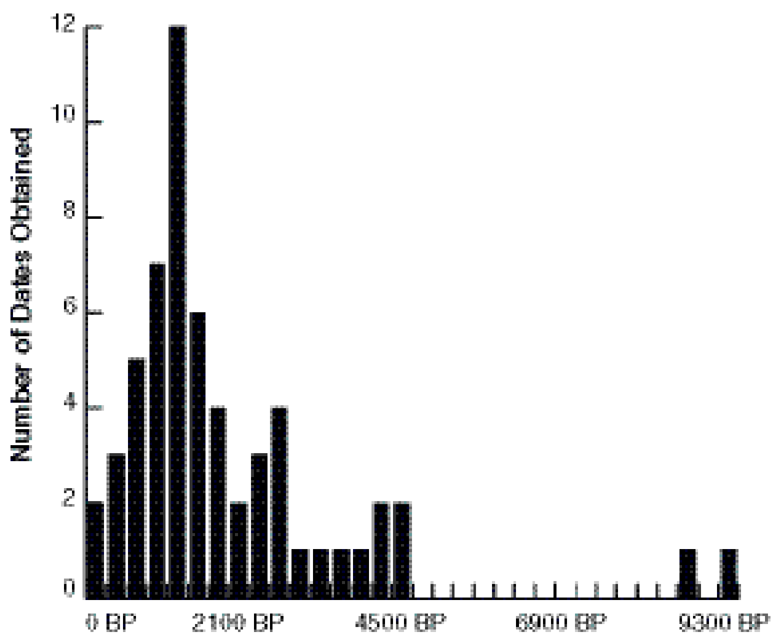

Figure 2. Frequency of radiocarbon dates for Yellowstone National Park in 300-year increments, beginning with AD 2000–1700 on the left.

The oldest recognized site in the park is the Osprey Beach site (48YE409), which represents occupation by the Cody Complex. It is called a complex because this "culture" is identifiable by more than one diagnostic artifact, including Scottsbluff and Eden points, and Cody knives (Figure 3). The radiocarbon date from the Osprey Beach site (48YE409) is represented in Figure 2 by the date on the far right of the chart at more than 9,000 years ago (Shortt 2001; see also Shortt, this volume). On the other end of the time scale, there are few dates (and sites) after 800–900 BP. The reasons for this are not clear, but the interior of the park may not have been as favorable for animals and humans due to the colder and snowier environmental conditions during the Little Ice Age (150-550 BP).

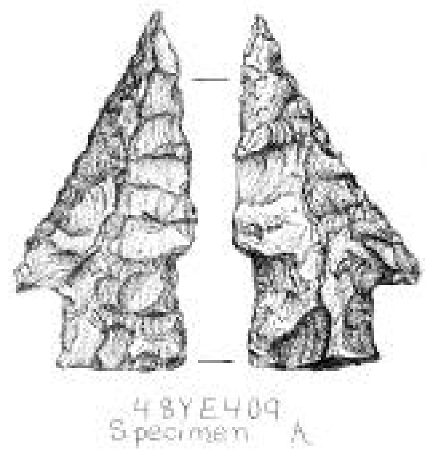

Figure 3. Cody knives from the Osprey Beach site.

Figure 4. Typical Pelican Lake projectile point.

The McKean Complex dates to about 3000 to 5500 BP and is well represented in sites around the lake. However, the most intensive use of the park dates from about 900 to 3000 BP (see the frequency peak in Figure 1); 78% of the dates fall within these time brackets. The Pelican Lake culture (Figure 4) is dated from 1800 to 3000 BP, and more sites in the park are identified as Pelican Lake culture than any other. The reasons for this period of intensive use are unknown, but this was also the time of the most intensive use of Glacier National Park. We speculate that environmental conditions must have been favorable during this time period. In recent years, there are more and complementary studies on the past environment, ranging from pollen, dendrochronology, and geomorphological age correlations with lake terraces. These all contain good information for the archeologist's interpretations.

Use of the Islands

Although there are archeological sites on six of the seven islands in Yellowstone Lake, the temporal parameters of this use are basically unknown. One reason for this is that the archeological resource has been severely affected by erosion and collecting. The islands were heavily used by the concessionaires, tourists, and park staff and their families during the 20th century and collection of Indian artifacts was a popular pastime.

One prehistoric campsite (48YE475) is contained within buried soil at Dot Island. Site 48YE475 has been severely damaged by erosion, but produced a radiocarbon date of 1500 ± 40 BP (Beta-157907). There is a bison bone deposit at the top of the buried soil that was previously identified as a paleontological site (Cannon 1996). The bone deposit was very compact, without taphonomic disturbance, and represented at least one animal. Because wave action has so severely eroded this deposit, it may never be possible to resolve whether this is a natural or cultural deposit of bison bone.

I am frequently asked, How did people get out to the islands? Did they walk out on the ice? That question presumes people were present in the winter. One wonders what resources people could find on the islands in the winter. Animals, of course, are able to cross on the ice and to swim back and forth to the lakeshore, but it is highly unlikely that people would swim out. This is not because of the distances, but because the cold water temperature could be expected to cause hypothermia. Various kinds of watercraft (canoes and rafts) might have been used.

As to why people went out there, the answer may be as simple as they were curious. We are unaware of any resources that would not have been available in greater quantities on the lakeshore.

Seasonality

As hinted at above, archeological sites have another aspect of time: seasonality, that is, the time of the year or season that the sites were occupied. Analysis of animal bones from archeological sites is the most common method of seasonal identification. However, few bones survive in the acidic soil around the lake, and other approaches, perhaps pollen analysis or identification of insects, will need to be used.

To date, we have not found any seasonal indicators for sites around the lake. This is not unusual because only four or five sites parkwide can be placed during a particular time of the year. Interestingly, these few sites all show early-spring to early-summer occupations. While it is premature to extrapolate from such a small data set to the lake area or to the entire park, it seems reasonable to suggest sites around the lake were used during the summer and into the fall. The archeological season-of-use data set will grow through time, and clearly illustrates the need for long-term research goals so that relevant data can be captured as they are identified.

If elk, deer, and bison stayed in the center of the park over the winter, then people would have been able to as well, because the limiting factor for human survival is availability of food resources. Winter travel would have been facilitated through the use of snowshoes. Today, some small groups of ungulates do not migrate out and those that successfully overwinter usually are found in thermally influenced areas. If bison and elk migrated to lower elevations for the winter prehistorically, with no political boundaries or developments to hinder their movement, we believe Precontact people would have followed. Typically, people time their movements around the landscape to match resource availability, such as fish spawning, the presence of camas and other edible bulbs, ripening fruit, and so on. Since Idaho obsidians are represented in tools found at sites on the lake, the seasonal movement model suggests that people wintered at lower elevations in Idaho and summered on the lake.

Site Types

Sites reflect the people and activities that created them, and can be interpreted by artifacts and other remains, such as hearths. Thus, archeologists classify sites into different types representing those activities.

Functionally, sites around the lake are dominated by base camps and sites where tools were manufactured or repaired. Base camps would be populated by extended family groups, young and old, men, women, and children. Most necessary living activities would take place there, and are represented by a wide variety of tools: projectile points, knives, scrapers, and perforators, and stone debris from their maintenance. Tools such as drills and perforators suggest manufacturing, possibly with leather and wood. Prehistoric pottery was first identified in the park at site 48YE449 and dates to about 500 BP. Base camps occupy favored locations around the lakeshore; these places were often used by many groups through time.

We do seem to find fewer end-scrapers than one might expect. If these are summer camps, the infrequency of these hide-working tools might suggest few hides were prepared in summer, when hair is thin and the hides would have to be carried to winter camp many miles distant.

There are few examples of kill sites in the park, in part due to the poor bone preservation in the generally acidic soil, but also because the topography does not lend itself to mass kills such as bison jumps. Instead, it is likely that one or more animals were taken by ambush at the tree–meadow juncture. It is possible that bison bone on the north shore of the lake (site 48YE697) represents a kill of an individual animal (Cannon et al. 1997). A problem with this interpretation is that the bison was basically not butchered, and the few flakes and tools found in association with the bones could have washed downslope from a campsite (48YE696). Also, lakeshore erosion removed an unknown amount of bone before the locality was documented.

We have little evidence for the types of shelters people may have used. No tipi rings (circles marked by the stones used to hold down the tipi cover) are known from around the lake, but due to the heavy ground cover they may be nearly impossible to identify. In the early historic period, conical timbered lodges (wickiups) were observed around Indian Pond (Norris 1880). In most cases, wickiups are temporary shelters for traveling groups (Kidwell 1974; Grinnell 1920).

Subsistence

As mentioned above, animal bone is rarely preserved in the acidic soil. Specialized analysis for blood residue left on tools provides clues about hunted animals. The standard suite of animals—rabbits, sheep, bison, canids—are present in the park from at least 9,000 years ago (Cannon et al. 1994; Shortt 2001). Grinding stones are usually assumed to represent plant processing, but a metate from site 48YE701 tested positive for deer antiserum and is interpreted as representing the processing of meat.

To date there is no evidence for prehistoric predation of fish around the lake, but relatively few excavations have been carried out and the fine screening of archeological sites necessary to recover such small bones has not been used. Because fish bone is small and fragile, there may be preservation and visibility problems. It is worth mentioning that flotation of hearth contents would recover fish bones if present, but the analyzed contents of seven such features have tested negative for fish.

Notched pebbles (net weights) are interpreted as evidence of weights used to hold fish nets in place. These can have either two or four notches, set opposite each other (in the case of two) or at 90 degrees from one another (in the case of four). Net weights have not been found around the lake, although some are known from the Yellowstone River close to Gardiner. Of course, specialized tools would not have been necessary to obtain or cook spawning cutthroat. While it may seem unusual to us, fish is one potential resource that many cultures do not define as food. The prehistoric use of fish is a matter of continuing investigation.

While there is some camas in the Lake horse pasture, this is marginal habitat and probably could not survive heavy collecting.

Stone, Tools, and Travel

Sites contain large amounts of fire-cracked rock, as well as debitage or flakes and shatter (broken flakes) that represent repair, manufacture and sharpening of tools. The fire- cracked rocks are derived from the local gravels, and are usually of the igneous varieties. These rocks would fracture in recognizable patterns after heating and cooling. Their presence represents hearth construction and stone boiling cooking of food.

The stone selected for tool production can be glossed as tool stone and includes a wide variety of different raw materials contained within the Absaroka glacial gravels as cobbles. The presence of tool-quality raw materials increased the attractiveness of the southern lakeshore and possibly increased the length of stay at these sites while tool kits were repaired and replenished. These gravels contain agates, petrified woods, quartzites, and volcanic tuffs: a grocery store for the flint knapper.

Volcanic tuff is similar in appearance to poor-grade obsidian and occurs as cobbles (both Huckleberry Tuff and Lava Creek Tuff). People were actively selecting these raw materials from which to manufacture tools. The tuff is typically black (or less often, red), opaque, and may have white crystalline inclusions. A geological source of this material is Park Point on the east lakeshore, but we don't understand the distribution nor do we know which parts of the geological exposure may have been used by people.

Questions about where people were before they came to the lake can in part be answered through the analysis of their tools: specifically, the sources of the stone. Archeological modeling suggests that people were familiar with resources in their home territory and would collect stone for new tools when near known geological exposures. Obsidian Cliff obsidian dominates tool assemblages throughout the park, although the percentages vary from area to area (Figure 5), so it is often the stone that occurs in smaller amounts that is more interesting.

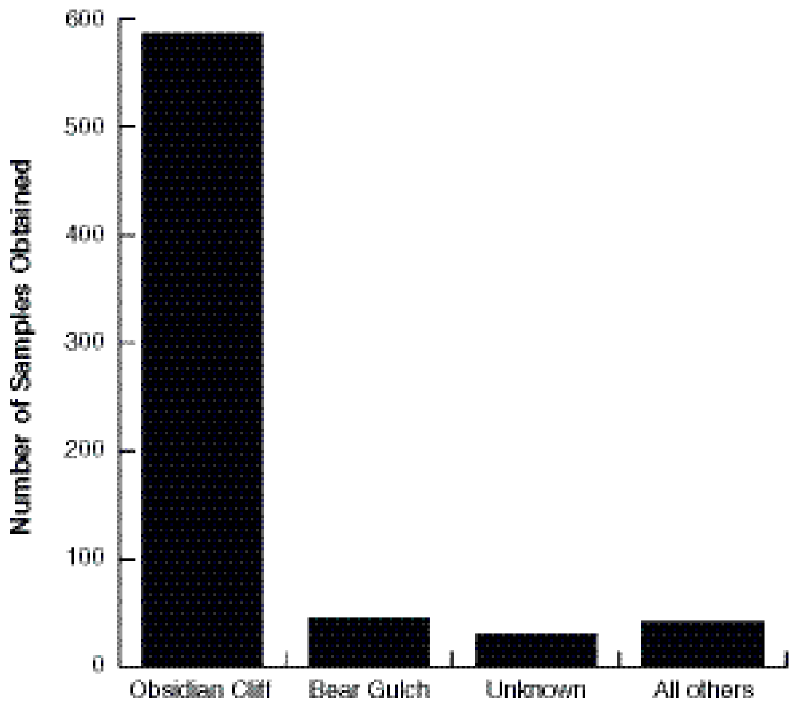

Figure 5. Obsidian sources in archeological artifacts in Yellowstone National Park.

We find evidence of contact or movement to and from Jackson Hole in the presence of tools manufactured from Teton Pass, Conant Creek, and Crescent H (south of Wilson, Wyoming) obsidians. These are limited, just as Obsidian Cliff obsidian is infrequently found in Jackson Hole. Packsaddle, Timber Butte, Malad, and Bear Gulch obsidians were imported into the park from Idaho. Bear Gulch was imported into the park in the highest amount and is second to Obsidian Cliff in popularity of use (Figure 5). Any analysis of a large sample of obsidian specimens results in some specimens with chemical fingerprints unlike any in the existing database, and we continue to seek samples of geological obsidians to add to the database.

As topography channeled early travel to a much greater degree than today, we are looking at mountain passes, river valleys, and lakeshores as transportation corridors. Through this line of inquiry we are investigating north–south prehistoric travel between Jackson Hole and Yellowstone, and between the park and Idaho, either over Jackson Pass, past Grassy Lake Reservoir, or down the Madison River valley. As people would obtain new obsidian for tools from sources along these routes, analysis of artifacts from Yellowstone Lake sites show where people had been. It is clear from tool and raw material analyses that people living on the southern lakeshore have very different territories (to the south into Jackson Hole and southwest into Idaho) from those around park headquarters, where there are greater relationships with the west and north.

Summary

Yellowstone Lake was important to people throughout prehistory because it is rich in plant, animal, and stone resources. The oldest sites in the park are known from around the lake. One of the reasons for this is the erosion that is exposing and destroying terrace deposits. On the positive side, because of this erosion, we have the opportunity to look "under the ground," to see cultural deposits that elsewhere in the park are deeply buried. At the present time, we interpret the archeological deposits around the lake as representing seasonal occupations where tool stone procurement, tool manufacture, and repair activities took place. As the basic outline of who used the park and lake area is understood, we can begin to ask better questions of our site data. Clearly, we are poised to make significant increases in our understanding and interpretations of the prehistoric human use of Yellowstone Lake.

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