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## Microbial Biodiversity of Great Salt Lake, Utah

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### ABSTRACT

Microbial biodiversity is difficult to measure in extreme environments due to the inability to culture many of the species, especially from hypersaline environments. Great Salt Lake (GSL), Utah, USA offers a unique ecology to study microbial diversity across a salt gradient. GSL has increasing salt from South to North that varies from marine salt concentrations to saturation, respectively. We used three methods to examine the biodiversity of the GSL—traditional cultivation on solid media, 16S rRNA gene sequencing, multiplexed 16S rRNA gene hybridization to the phylochip, and DNA hybridization to the Geochip for metabolic diversity estimates. Over 40 isolates from the North Arm were obtained, while six were selected for identification. Isolates included gammaproteobacteria, bacilli, and actinobacteria. Sequencing the 16S rRNA genes for identification yielded 350 clones. Rarefaction curves indicated that this did not represent the bacterial diversity of the GSL, while estimation of the diversity with the Affymetrix phylochip produced over 1000 different genera in 31 different families. Estimation of the metabolic diversity found that genes for each activity were present in all three locations. The gene abundance was similar in all locations, except for metal use where the gene abundance declined as the salt gradient declined. This study provides the first evidence of the large microbial diversity supported by GSL to provide a large metabolic potential independent of the salt concentration.

### INTRODUCTION

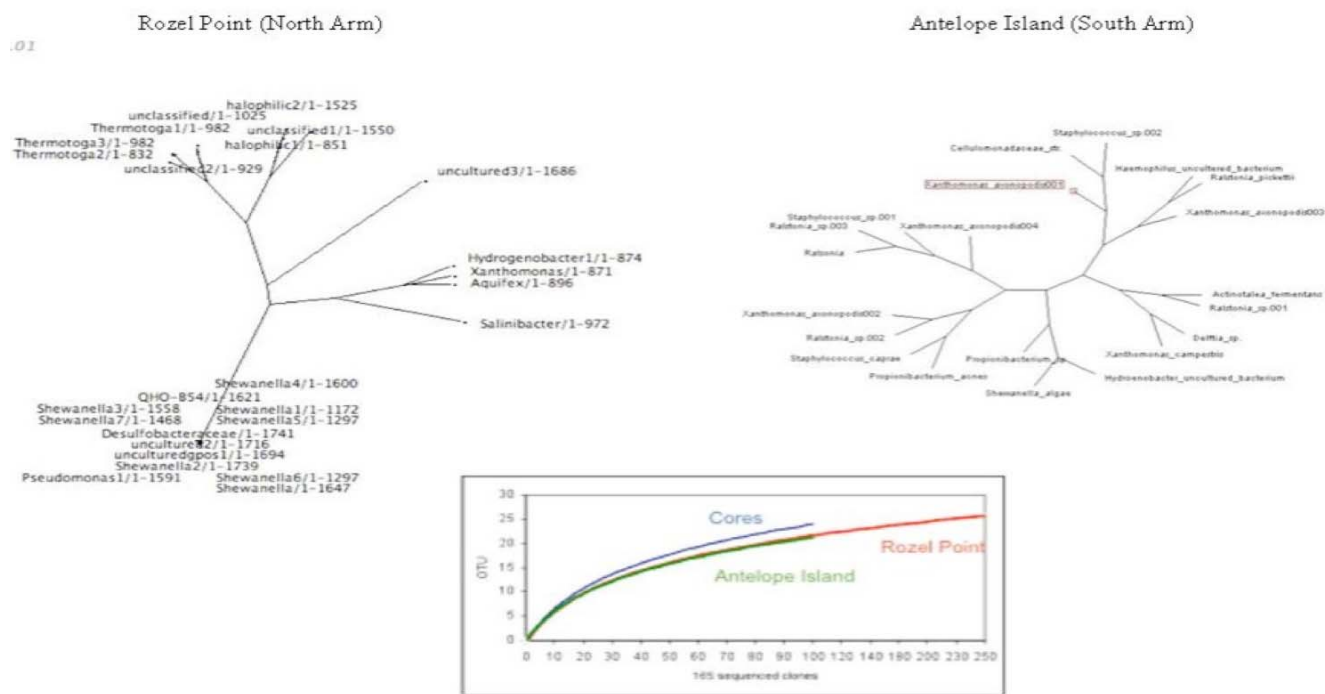
Approximately  $1.5 \times 10^4$  years ago, Lake Bonneville, a late Pleistocene lake, reached a size of  $5.2 \times 10^4$  km<sup>2</sup> before suddenly discharging an immense volume of water to the north into what is now Utah and Idaho. This flood was caused by capture of the Bear River, which greatly increased the supply of water to the Bonneville Basin. Today's Great Salt Lake (GSL) is a large remnant of the ancient Lake Bonneville, and occupies the lowest depression in the Great Basin. GSL is the largest U.S. lake West of the Mississippi River, the 4th largest terminal lake in the world, and the world's second most saline lake

(Hassibe & Keck 1993; Stephens 1997; Aldrich & Paul 2002; Gwynn 2002).

Much of the salt contained in GSL was originally in the water of Lake Bonneville. Today, about two million tons of dissolved salts enter the lake each year. While GSL is typically 3- to 5-times more saline than the ocean, with the exception of sulfate, it contains roughly the same mixture of salts (Gwynn 2002). In contrast to the divalent cation-rich Dead Sea (Post 1977), GSL is a sodium chloride lake with an exceptionally high sulfate concentration (10-20 g/l) (Whelan 1973).

Industrialization of the Wasatch Front, a 100 mile-long urban corridor stretching from the cities of Provo to Ogden, led to utilization of GSL for recreation, agriculture, mining, oil exploration, railroad connection, and brine shrimp harvests. The GSL ecosystem receives industrial, urban, mining, and agricultural discharge from a  $3.8 \times 10^4$  km<sup>2</sup> watershed inhabited by more than 1.8 million people. To meet the demands of industrialization, an East-West railroad causeway was completed across the lake in 1959 (Waddell & Bolke 1973; Cannon & Cannon 2002). The causeway restricts the movement the water between the North and South arms, effectively dividing the lake into two ecosystems based on the salt gradient.

Freshwater flows into the lake in the South Arm via three rivers. Adjacent to the causeway, the South Arm has a salinity of ~17% - about four times saltier than the ocean. The North Arm has no significant freshwater influx and is become saturated with the salt concentration nearing 27-30%. With construction of the causeway, GSL has become at least two different ecosystems linked through breaches in the causeway to create a halocline in two dimensions. The NaCl concentration changes from North to South as well as with depth, known as the "deep brine layer". The size of the deep brine layer changes with local environmental conditions, such as temperature and wind speed. The fluid dynamics of the halocline restricts the mixing, thereby creating multiple non-homogeneous environments of varying NaCl concentrations across the Lake from North to South and from surface to sediments.



**Figure 1**–Diversity of the organisms determined using a DNA library from the total DNA isolation from two locations in GSL based on the salt concentration. Each sequence was determined using a full-length sequence of the 16S rRNA gene. The rarefaction curve was done for each location and compared to the GSL core sample from 100 cm. In all cases, the diversity was not adequately sampled to accurately determine the microbial diversity in the location.

The lake offers a variety of unique microenvironments (e.g. petroleum seeps, thermal springs, salt and freshwater springs, mudflats, deep brine layers, and deep sediments that date to prehistoric Lake Bonneville). Each of these conditions found in the lake offers interesting combinations of physical, chemical, and biological features that are linked to salinity as a spatial and temporal variable that creates gradient and boundary effects. Together, these physical and biological features shape the overall flora and fauna of GSL today.

The extent of human interaction with GSL also adds a new dimension to the study of the microbial ecology of GSL. These features make GSL a unique environment that is understudied with respect to the microbiota that underpin the ecological web in the lake, especially the geochemical cycling specific to the heavy metal and sulfur content of this unique ecosystem. The diverse conditions and gradients of salinity, temperature, and other physical features are the motivations to examine the GSL nutrient and element cycles in the context of the lake’s genetic potential and metabolic interactions between the living communities of the lake.

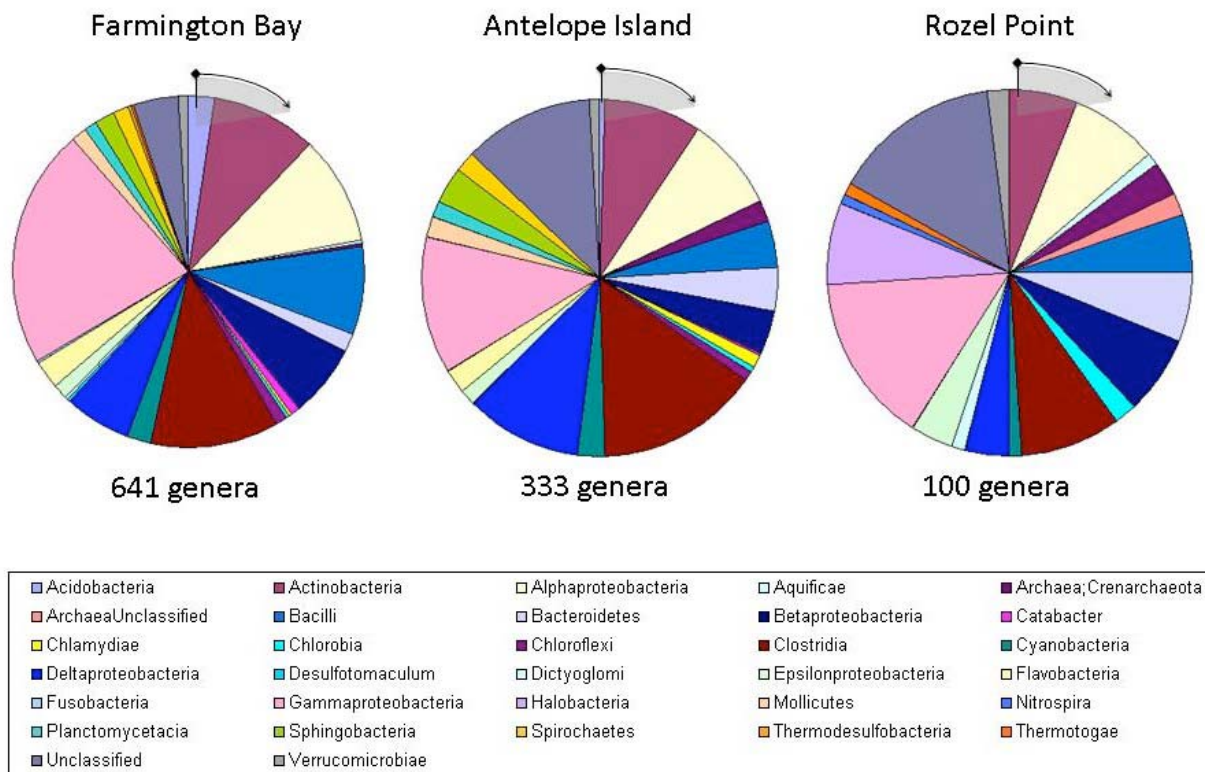
We initiated experiments to determine the microbial diversity in GSL with the larger goal of understanding

microbial metabolism and survival across the salt gradient. We hypothesized that the microbial diversity would be low and dominated by relatively few types of organisms. However, we determined the microbe population to be rich and diverse with little variation along the salt gradient between families of microbes. Specific strain diversity changed between the study sites with an increase in archaea as the salt content increased. This study found that GSL supports a diversity of microbes with the metabolic diversity to maintain metabolic activity at all study sites around the lake.

## MATERIALS AND METHODS

### Sample Collection

In the summer of 2007, water samples were collected from different sites throughout GSL: in the North Arm at Rozel Point (saturated salt), in the South Arm at Antelope Island (17% salt) and at Farmington Bay (10% salt). Samples were collected in sterile 4 l plastic bottles (Nalgene, Fisher Scientific, CA). In addition, 50 ml of sample from each site was collected in sterile tubes with minimal headspace for subsequent compound analysis. Within 6 hours of collection, samples were refrigerated at 4°C until processing.



**Figure 2**—Microbial diversity of three locations in GSL using the phylochip. The arrows indicate the start point (short bar) and the direction of the legend (arrow around the pie chart). The legend is organized from left to right in rows.

### Bacterial Isolation

The water and sediment samples from each location were plated on LB (Difco, MI) agar and incubated overnight at 30°C. Colonies on the plates were picked, re-streaked on new LB agar, and checked for purity by performing a Gram-stain and visual inspection of individual colonies.

### DNA Isolation

Total genomic DNA from the hypersaline waters of GSL was extracted utilizing a modified protocol published by Griffiths et al. (2000). Briefly, 1 gallon (3.85 l) of water collected from GSL was centrifuged (10000 x g, 40 min, 4°C) in a Sorvall high-speed centrifuge and the cell pellet resuspended in 500 µl of modified CTAB (hexadecyltrimethylammonium bromide) extraction buffer (equal volumes of 10% CTAB in 0.7 M NaCl with 240 mM potassium phosphate [pH 8]). Bead beating was used to lyse cells and DNA was extracted with chloroform and precipitated with sodium acetate and ethanol. The extracted community DNA was purified through a Sephadryl S-300 column. Briefly, the column was constructed by plugging a 5 ml syringe with sterile glass wool, pouring 5 ml of resin suspended in 24% ethanol into the syringe and centrifuging 10 minutes at 1000 x g at room temperature. The column

was washed twice with sterile ddH<sub>2</sub>O. Community DNA samples were added to the column and purified by centrifugation for 10 minutes at 1000 x g at room temperature.

### 16S rRNA Gene Sequencing

To assess microbial diversity DNA was extracted using a modified protocol described by Griffiths et al. (2000). The extracted DNA was purified by passing it through a Sephadryl S-300 column and used to amplify the 16S rRNA gene using Archaea or Bacteria universal primers. The products were sequenced at the Center for Integrated BioSystems Genomics Core (CIB) (Logan, UT).

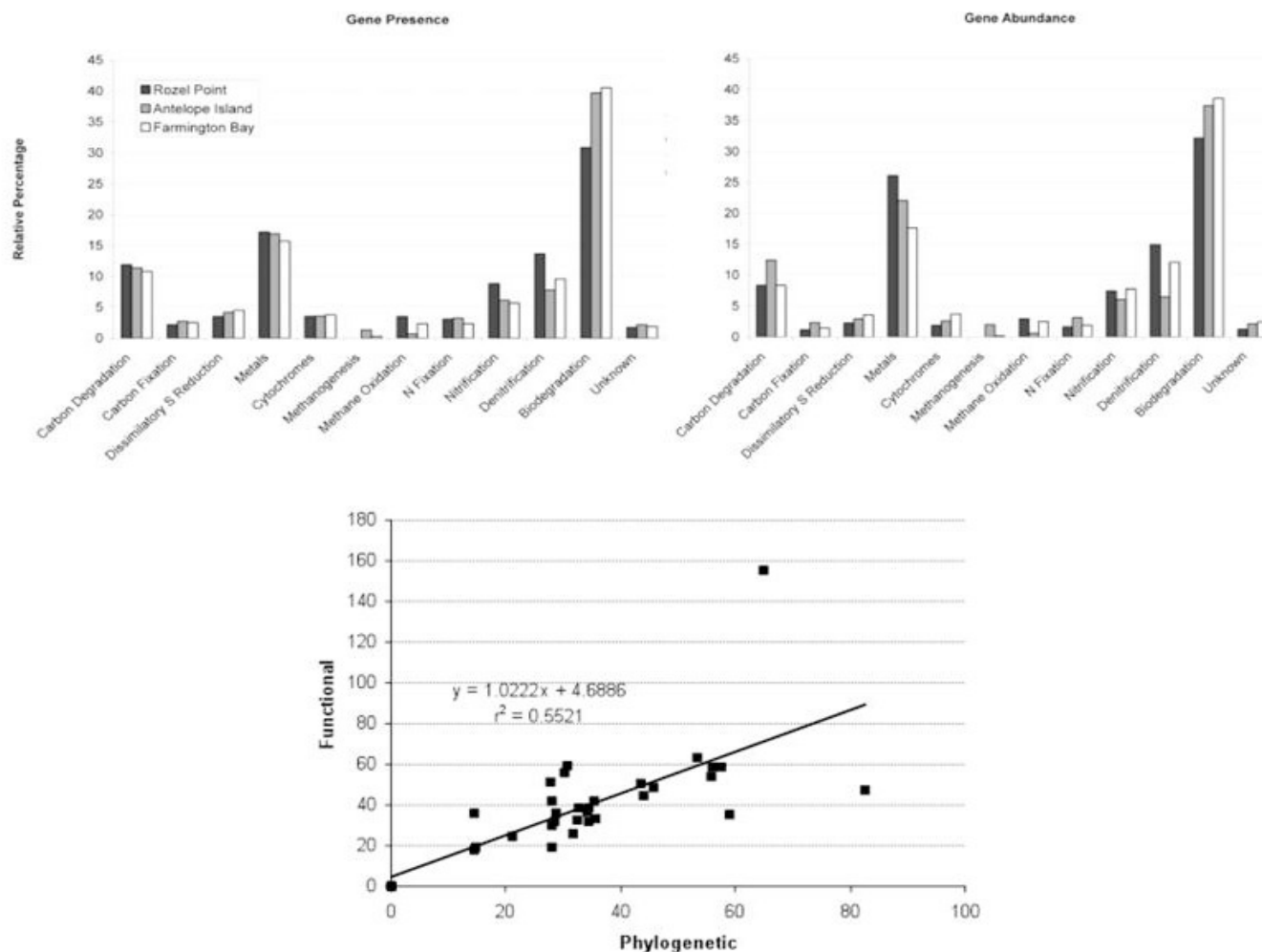
### Phylochip Analysis

We used the 16S Phylogenetic Array (phylochip; Affymetrix, Santa Rosa, CA, USA) containing probes for 8741 Bacterial and Archaeal taxa as described by Brodie et al. (2007). Hybridization of the phylochip is achieved using slightly modified Affymetrix protocols. Briefly, the 16S rRNA genes were amplified by PCR with Bacteria (F: 5'-AGAGTTTGATCCTGGCTCAG-3', R: 5'-ACGGCTACCTTGT AGCACTT-3') or Archaea (F: 5'-GACGGCGGTGTGTCA-3', R: 5'-GCGGATCCGGCCGCTGCAGAYC-3') specific

primers. To minimize the primer bias, PCR amplification was performed with a temperature gradient from 48°C to 58°C for the annealing temperature. The PCR products from the different amplification reactions were collected, purified and quantified. The rRNA (200 ng) amplicon was fragmented by DNaseI digestion for 20 minutes at 25°C. The DNaseI was inactivated and the fragmented DNA biotin labeled for 60 minutes at 37°C following the Affymetrix protocol. The labeled DNA was added to Affymetrix hybridization solution and hybridized to a phylochip for 16 hours at 48°C rotating at 60 rpm. The chip was washed and stained following the Affymetrix protocol and scanned utilizing an Affymetrix ChiScanner 3000 at the CIB Affymetrix Core Laboratory. The hybridization intensity values and probe set annotations were merged (.gif file). The chips were normalized with R with robust multichip average (RMA) (Irizarry et al. 2003).

### Statistical Analysis and Data Visualization

RMA normalized data were analyzed using SAM (Version 2.01) (Tusher et al. 2001) with a one class time course experimental design using the xCluster R module (Center for Integrated BioSystems, Logan, UT; <http://cib-xcluster.biotech.usu.edu/>). The gene expression changes were transformed to the log<sub>2</sub> ratio, and were calculated by determining the difference in log<sub>2</sub> intensity of a single time point with the preceding time point. Any gene with a log<sub>2</sub> ratio of at least ± 0.58, which is equivalent to a ±1.5 fold change, and q < 0.3 was considered significant (Storey & Tibshirani 2003). The entire experiment was completed in two biological replicates.



**Figure 3**—Estimation of the biological processes in GSL using the GeoChip. Gene presence was determined by a hybridization event, while the gene abundance was determined by measuring the hybridization intensity on the chip. Estimation of the connection between the GeoChip and phylochip is depicted as the correlation between the functional and phylogenetic assays, respectively.

**Table 1**—Bacterial isolates from the North Arm of GSL.

Predicted Identification <sup>1</sup>	Sample location	Linage	Identity to 16S rRNA sequence (%) <sup>2</sup>	Phylochip probe set hybridization identification (FB:AI:RP ratio) <sup>3</sup>
<i>Micrococcus luteus</i>	Rozel Point (CL1)	Actinobacteria; Micrococcaceae	99	HN2-11 (1.8:1.2:1) B-P26 (1:1:1)
<i>Salinivibrio costicola</i>	Rozel Point (MC-A)	Gammaproteobacteria; Vibrionales	99	DSM8285 (1.5:2.1:1) ATCC35508T (0.8:1:1)
<i>Morganella morganii</i>	Rozel Point (C-2)	Gammaproteobacteria; Enterobacteriaceae	98	C3 (1:1:1) AP28/C5 (1.7:1.7:1) Ju27C4 (1.4:1.2:1) Sludge (1.3:1.3:1) ATCC35200 (1.2:1.2:1)
<i>Planococcus maritimus</i>	Rozel Point (CL2)	Bacilli (Firmicutes); Planococcaceae	97	TF-9 (1.4:1.5:1)
<i>Halomonas venusta</i> -like	Rozel Point (MC-B)	Gammaproteobacteria; Halomonadaceae	77	17 <i>Halomonas</i> found. This species was not represented on the chip.
<i>Morganella morganii</i> -like	Rozel Point (RC-1)	Gammaproteobacteria; Enterobacteriaceae	54	C3 (1:1:1) AP28/C5 (1.7:1.7:1) Ju27C4 (1.4:1.2:1) Sludge (1.3:1.3:1) ATCC35200 (1.2:1.2:1)

<sup>1</sup>Identification was based on the full-length identity from the closest match. We defined that a tentative identification was limited to the identity measure listed in the table. <sup>2</sup>Based on full-length sequence. <sup>3</sup>FB = Farmington Bay, AI = Antelope Island, RP = Rozel Point; Probe set identifications are denoted as annotated on the Phylochip. In all cases the probe set was used for the lineage identification.

## GeoChip Analysis

To determine the functional genomic capabilities of the microbial communities within the GSL, we used the GeoChip functional gene array (Zhou et al. 2002; He et al. 2007). Extracted community DNA (no amplification step) was labeled with cystidine-5 (Cy-5) dye prior to hybridization. Briefly, approximately 2 mg of genomic DNA was denatured for 5 minutes at 99.9°C in solution with 0.1 mM spermidine and random octamer mix (Invitrogen, Carlsbad, CA, USA) and snap chilled on ice. Following denaturation, 2.5 mM dithiothreitol (DTT), 0.25 mM dATP, dCTP and dGTP, 0.125 mM dTTP, 0.125 mM Cy5-dUTP, and 80 U Klenow fragment (Invitrogen) were added. Reaction mixtures were incubated at 37°C overnight. Labeled target DNA was purified with a QIAquick PCR kit (Qiagen, Valencia, CA, USA) according to the manufacturer's instructions. Labeled DNA was measured on a ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE) and dried using a speed-vac at 45°C for 45 minutes. Dried, labeled DNA was resuspended in a solution of 50% formamide, 5 x sodium saline citrate (SSC), 0.1% sodium dodecyl sulfate (SDS), 0.1 µg µl<sup>-1</sup> salmon sperm DNA and 0.02 mM spermidine and incubated at 95°C for 5 minutes. Labeled reactions were kept at 60°C until hybridization. Community DNA hybridizations were performed using a HS4800

Hybridization Station (TECAN US, Durham, NC) and hybridization conditions were followed as indicated elsewhere (Yergeau et al. 2007). GeoChip microarrays were scanned using a ProScanArray microarray scanner (PerkinElmer, Boston, MA) as mentioned by Yergeau et al. (2007). Scanned images were analyzed using ImaGene 6.0 software (BioDiscovery, El Segundo, CA, USA). GeoChip array results were normalized as established by Yergeau et al. (2007).

## RESULTS AND DISCUSSION

### Bacterial Isolation

The initial experiments attempted to isolate organisms from multiple locations in GSL. We obtained 40 bacterial isolates from all locations that varied in colony color, size, and morphology. Six of the isolates were selected for identification using 16S rRNA gene sequencing (Table 1). Full-length sequence indicated that two new isolates were found that were identified to be *Halomonas venusta* and *Morganella morganii* (Table 1). The isolates represented members of the Actinobacteria, Gammaproteobacteria, and Firmicutes. Isolation attempts provided only organisms that we capable of growing on common, but nutrient restricted agar-LB or marine agar. Since the media and growth conditions were limited, the number and type of colonies

likely under-represented the total number of microbes capable of growth from GSL. This is also supported by the fact that what we isolated did not match isolates from studies, but are possible from this environment.

### Phylogenetic Diversity Measure

The ease with which we isolated different organisms from the North Arm led us to question the diversity estimate of our sample locations in GSL—Rozel Point (North Arm) and Antelope Island (South Arm), and Farmington Bay (South Arm). To provide a larger view of the microbe population in GSL we turned to growth-independent methods. Examination of the microbial community in each location was done using total DNA isolation, cloning, and 16S rRNA gene fragment sequencing. The 16S rRNA gene sequences showed presence of numerous distinctly different organisms between the North Arm and the South Arm, but only different types of organisms were found at each location (Figure 1). This led to an estimation of the diversity using rarefaction curves for each location. The operational taxonomic unit (OTU) estimation was rising after 100 samples from the South Arm and 250 samples from the North Arm, suggesting our hypothesis that the total diversity was underestimated by the sequencing effort. The diversity of GSL was unexpectedly high, even in saturated NaCl of the North Arm. Interestingly, none of the organisms we isolated were found in the 16S rRNA gene sequencing experiment. Based on these observations, we determined that the amount of DNA sequencing needed to estimate the total diversity in the GSL was not possible with this approach. Consequently, we used an alternative approach to measure the bacterial diversity on a larger scale.

To re-estimate the microbial diversity in GSL we used the phylochip that contains over 8500 probe sets, which estimates the diversity based on hybridization of the 16S rRNA genes to the chip. The estimate for microbial diversity was done at three locations with varying salt concentrations—Farmington Bay (6% NaCl), Antelope Island (12% NaCl), and Rozel Point (30% NaCl). Similar microbial families were represented in each location, but individual genera representation decreased with increasing salinity from 641 genera to 100 genera at Rozel Point (Figure 2). In all cases the families for the isolates found in this study were represented in all locations. The organisms found with 16S rRNA gene sequencing were also observed based on hybridization of the total DNA isolated from each location to the phylochip. Since all the previous data were included in these data we concluded that the phylochip more accurately represented the community in GSL, while the isolated cultures and 16S rRNA gene sequence alone substantially underestimated the overall diversity of GSL.

In all sample locations the diversity was larger than expected. To adequately estimate the true diversity it would be better to use a metagenomics approach, which we are doing as part of the larger project.

A number of different patterns were observed in the community dynamics due to changes in salt concentration. Most of the phyla were found in each location, such as actinobacteria, cyanobacteria, and proteobacteria; yet the hybridization intensity for specific genera changed with increasing salt. The signal intensity is a measure of the population proportion as increasing amounts of the 16S rRNA gene leads to an estimation of the proportion of the community. Consequently, we estimated the ratio of the isolates found in each location based on the signal intensity between the locations relative to Rozel Point (Table 1). In all cases the salt concentration is inversely proportional to the signal intensity ratios. At the family level, this trend did not hold true. For example, Deltaproteobacteria contained the most genera at Antelope Island and as the salt concentration increased genera of this class decreased.

New phyla appeared with increasing salt, such as Chlorobia, which was found in Farmington Bay in a small amount and it increased with the salt concentration. In other cases some families were only found in the North Arm sample (Rozel Point) - Archaea and halobacteria, as expected. In other cases specific families were at specific locations. For example, large populations of Chlamydiae were only found at Antelope Island, while *Desulfotomaculum* and *Thermodesulfobacterium* were found only in Farmington Bay. Other specific examples were found where individual organisms changed differently to that of the entire family. The community dynamics observed by investigating individual probe sets within a specific family was far more extensive than culture isolation or 16S rRNA gene sequencing predicted and we expected. We suspect that these changes represent the specific gene content of a species or strain that represent the unique metabolic processes that allow survival and growth within the stress of salt concentration.

### Metabolic Diversity

The amount of community membership change observed with the phylochip led us to question the amount of metabolic diversity in the community across the salt gradient, which may begin to explain changes of individuals within a family. To broadly measure the metabolic potential of the total community DNA was hybridized from the sample locations to the Geochip. Hybridization indicated presence of the metabolic gene as



represented on the chip. In some cases, the chip contained extensive genetic diversity for single genes, while other genes for intermediary metabolic processes were only partially represented (He et al. 2007). We did not estimate the amount of expression in this study, but rather presence of the gene as an estimate of the metabolic potential. The magnitude of the signal was used to estimate the relative abundance of that gene in the community.

In all locations the metabolic presence and abundance were similar (Figure 3). Abundance of the Geochip signal provided an estimate of the number genes in a broad metabolic category. This is highlighted by the striking similarity between the gene abundance and the gene presence (Figure 3). Metal metabolism is the only category that was counter to this trend. Genes for metal use were present in all locations, but the number of genes declined ~25% as the salt concentration declined, with the lowest abundance observed in Farmington Bay. This observation suggests that the diversity of the genes for metal use become more homogenous as the salt concentration declined.

Rozel Point contained more genes for metal and nitrogen metabolism compared to the other locations. Genes for methanogenesis were not detected at Rozel Point, but were found at low intensity values in the other two locations. The similarity in presence and abundance indicates that the entire community has about the same metabolic potential in the gene content. Realization of the metabolic potential depends on the gene expression regulation for each location and the specific local conditions, which was not measured in this study.

Predictive value of the phylogenetic and metabolic estimates in combination was limited. The correlation between the two factors explained just over half of the variation ( $r^2 = 0.55$ ), indicating that the phylogenetic diversity was not strongly correlated to the metabolic capability. Consequently, the community metabolism based on the community membership was not estimated. This observation is congruent to that of Zhou et al. (2002) where use of the Geochip in soil failed to predict the microbial diversity as well.

In conclusion, this study determined that culture methods found only a very small limited number of the families present at Rozel Point. Estimation of the phylogenetic diversity with 16S rRNA gene sequencing was limited to the depth of coverage and inadequate to fully predict the biodiversity of GSL. Use of high through put chip

technologies found extensive diversity of organisms and metabolism. Estimation of the metabolic diversity of the community found an unexpected amount of metabolism occurring at Rozel Point, indicating that GSL has a very active and diverse microbial community that has broad capabilities to consume and produce compounds from microbial metabolism.

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Great Salt Lake, Utah east of the Wasatch Mountains, Utah. This photo is taken from the International Space Station from approximately 380 km. The railway clearly separates the north and south sections of the lake, which have different salt concentrations due to the barrier. The water level of the lake is very low: note how the northeast arm of the lake has disappeared, and how Antelope Island isn't an island at all. Date: 19 August 2003. Wikimedia Commons at [en.wikipedia.org](http://en.wikipedia.org). Accessed February 2009.