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Hypersaline Lake Environments Exhibit Reduced Microbial Dormancy

Joshua Christopher Vert

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Master of Science

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ABSTRACT

Hypersaline Lake Environments Exhibit Reduced Microbial Dormancy

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From acid seeps and deep-sea thermal vents to glacial ice and hypersaline lakes, extreme environments contain relatively simplified communities consisting of extremophiles that have evolved to survive and thrive under adverse abiotic conditions. In more neutral environments, microorganisms use dormancy as a common life history strategy to weather temporal fluctuations of resources or stresses until more ‘optimal’ conditions are present. It is unclear if dormancy is an essential survival mechanism for microorganisms in extreme environments; however, recent studies suggest that extreme environments may create stable conditions for extremophiles to the extent that dormancy is of less ecological importance. Using lake salinity levels as measurements of “extreme,” we evaluated the dormancy of bacterial and archaeal phyla and lake chemistry in five hypersaline and five freshwater lakes across the western United States. Dormancy was calculated using targeted metagenomics to analyze 16S rDNA and rRNA tag sequences. It was hypothesized that bacteria and archaea in hypersaline lake communities would exhibit lower levels dormancy than bacterial and archaeal communities in geologically similar freshwater lake controls. It was also hypothesized that microbial dormancy would decrease as the dominant extreme environmental variable increased in the lakes. As hypothesized, overall dormancy decreased at least 2-fold in hypersaline compared to freshwater lakes for both bacteria and archaea. Of the predominant phyla and subclasses, Firmicutes, Bacteroidetes, and Gammaproteobacteria each demonstrated at least a seven-fold decrease in dormancy in hypersaline lakes compared to freshwater lakes. Specifically, species within the genus *Clostridium* were responsible for 85% of the dormancy observed in the phylum Firmicutes. Also as hypothesized, microbial dormancy decreased as salinity increased in the lakes. Lower dormancy in hypersaline lakes correlated with increasing salinity while lower dormancy in freshwater lakes correlated with increasing total phosphorus levels. These results suggest that dormancy is a less common life history strategy for microorganisms in extreme environments; it is proposed that this is due to the relatively stable environment in hypersaline lakes and the reduced number of available microbial niches. These results also suggest that the dominant extreme stress (i.e., salinity) may override other driving factors in an environment to ultimately determine microbial community composition, diversity and richness.

Keywords: niche differentiation, archaea, bacteria, 454 pyrosequencing, 16S, targeted metagenomics, phosphorus, extremophiles

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1. INTRODUCTION

1.1 Microbial Ecology

Over the past 20 years, advances in molecular techniques have allowed the “black box” of microbial ecology to be pried open. The phylogenetic information of thousands of the bacteria, archaea, and eukaryotes are now available from a wide range of habitats, including the open ocean (Venter *et al.* 2004), acid mine drainage sites (Tyson *et al.* 2004), the human microbiome (Gill *et al.* 2006), sewage sludge reactors (Martin *et al.* 2006), and soils (Tringe *et al.* 2005). Although it is difficult to analyze ecological significance through the immense diversity of bacteria and archaea species, it is suspected that they obey the same ecological “rules” as plant and animal communities (Martiny *et al.* 2006; Horner-Devine and Bohannan 2006). For example: bacteria and archaeal diversity is directly related to ecosystem stability (Cleland 2012, Finlay 1997); rare or keystone species exist that are essential to ecosystem function and diversity such that microorganisms have developed a myriad of life history strategies to contend with fluctuating environmental conditions (i.e., dormancy, microevolution events, and resting-growth strategies, Martiny *et al.* 2006). Most of these working theories apply to environments that are subjected to abiotic and biotic environmental fluctuations but do these ecological theories also apply in extreme environments?

1.2 Extreme Environments and Extremophiles

Microorganisms are extremely diverse and account for approximately 60% of earth’s biomass and biodiversity (Fraser 2000) and offer a unique setting to investigate microecology (Martiny *et al.* 2006, Rothschild *et al.* 2001). As a whole, extreme environments contain relatively simplified microbial communities of extremophiles (i.e., thermophiles, halophiles,

xerophiles, and thermoacidophiles) that have often evolved specific life history strategies to survive in their environment (Fiser *et al.* 2012, Oren 2002). For example, in the sands of the Atacama Desert, known as the world's driest desert, microorganisms experience some of the highest solar UV index ever recorded (Warren-Rhodes *et al.* 2006). The microbial communities in the Atacama Desert have a relatively simplified structure consisting largely of anaerobes; they have thicker cell walls to prevent desiccation and have one of the most advanced DNA repair mechanisms (Navarro-Gonzalez *et al.* 2003). In the water of the Dead Sea, the deepest hypersaline lake in the world, bacteria and archaea experience an extremely hypertonic environment (Garfinkle *et al.* 1996, Shani *et al.* 1987). The microbial communities are also relatively simplified, consisting primarily of a few species of halophiles (Baliga *et al.* 2004). A majority of the microorganisms have a reduced number of thymines (a UV "target"), colorful photoprotective carotenoids, compact cell surface proteins and the ability to increase osmolarity in the cytoplasm to prevent any loss of water to the external environment (Nissenbaum 1975). All of these environments contain microorganisms that have evolved to survive and thrive in environmental conditions outside of the moderate parameters that make up a majority of the biosphere (i.e., temperature of 15-40 °C, pH 7.4, salinity from 0.05% to 3%, and 1 atm pressure, Canganella *et al.* 2011). Understanding how these microorganisms interact with their environment remains a central theme of microbial ecology.

Hypersaline lakes also offer a simplified system to study bacterial and archaeal interactions with each other and the environment (Ollivier *et al.* 1994). Hypersaline lake chemistry is even more simplified compared to other extreme environments (Boutaiba *et al.* 2011) since hypersaline lakes are often formed by the same hydrological processes. These lakes contain a high concentration of sodium, magnesium, bromide, chloride, or calcium ions –

typically exceeding that of the ocean (3.5%, Kerr *et al.* 2001). They form when runoff or other sources of water containing high concentrations of salt flow into an endorheic (i.e., terminal) lake. Because there is no lake outlet, evaporation concentrates the dissolved salts. Additionally, hypersaline lakes can also form when bedrock containing high concentrations of salt within the lake is intercepted by subsurface flow, increasing the salinity of the lake regardless of the lake's feed water or outlets (Rodríguez-Valera *et al.* 1981).

1.3 Dormancy

A common life history strategy for microorganisms is dormancy (Kaprelyants *et al.* 1993). Microbial dormancy is the ability to reduce metabolic activity until conditions favor increased growth rates. A microorganism can accomplish dormancy through many strategies that include: formation of cysts, formation of endospores, or simply suspending normal metabolic activity (Lennon *et al.* 2011). We see examples of dormancy in plants and animals. Higher plant species use seed banks and species within the animal kingdom may undergo hibernation, brumation, aestivation, and diapause (Pake *et al.* 1996, Lyman *et al.* 1955). As with plant and animal ecology, microbial dormancy may be triggered by a fluctuation of environmental conditions and even fluctuations over time (Sussman *et al.* 1973). In the bacterial and archaeal world, dormant microorganisms become a microbial bank, much like the seed bank of higher plants, waiting to resume normal metabolic activity with little damage or change to their DNA (Stolpovsky *et al.* 2011). As microorganisms emerge from dormancy, changes in microbial community composition may regulate specific ecological processes such as methanogenesis, sulfate reduction, and nitrification. Microbial dormancy has also been shown to alter patterns of succession and the maintenance of biodiversity (Jones *et al.* 2010). The ecological importance of dormancy is apparent in more neutral environments but it remains

unclear if dormancy even occurs in extreme environments where one or multiple extreme conditions are constant and do not fluctuate significantly. Furthermore, there is a question of whether a bank of microorganisms present in extreme environments avoid stress and await for more optimal environmental conditions (Stevenson 1978).

1.4 Extreme Environments and Microbial Niches

Bacterial productivity in freshwater aquatic environments is strongly driven by concentrations of phosphorus (Schindler 1978). Subsequently, bacterial dormancy decreases with increasing total phosphorus and helps to the maintain diversity (Jones *et al.* 2010). Consequently, fluctuations in resources can largely affect the levels of dormancy in a given microbial community (Sussman *et al.* 1973). An extreme environmental driver, such as salinity; however, may overshadow resources that normally drive microbial community structures in neutral environments. Hypersaline environments stay relatively constant on a temporal scale (Cytryn *et al.* 2000, Stephens 1990, Williams *et al.* 1990). Even microorganisms in the Great Salt Lake, UT, a hypersaline lake that experiences some of the highest fluctuations in salt concentration (lake area fluctuations between 937 square miles and 2,300 square miles; salinity fluctuations between 8% and 33.5%), still experience an extremely hypersaline environment throughout the calendar year (Stephens 1990). In hypersaline lakes, although other resources shift over time, salt concentrations tend to be a constantly high and overriding driving factor regardless of other temporal variations (Verschuren *et al.* 2004).

Although microorganisms influence ecosystem processes across a large landscape, extremophiles still inhabit and interact in a defined space (Lennon *et al.* 2012). As an evolutionary effect of interaction and often times competition, microorganisms are often driven

to develop different patterns of resource use and to occupy different niches to reduce out-competition – this is known as niche differentiation theory (Finke *et al.* 2008). Niche differentiation has become a widely accepted theory of cohabitation in environments (Leibold *et al.* 2006, Hubbell 2006). It explains how natural selection in moderate environments drive competing species to use different resources and, by default, to occupy different niches. It explains how species cohabitation and can push microorganisms into higher levels of activity or even cause periods of dormancy (Rojas *et al.* 2008). However, the niche differentiation theory is specific to environments with multiple sources of energy for a variety of species. When we apply the same theory to extreme environments, mathematical models tend to fail (Dumbrell *et al.* 2010).

1.5 Experimental Approach

In this study, bacterial and archaeal dormancy was evaluated and dormancy was linked to environmental conditions in five freshwater and five hypersaline lakes across the western United States. The dormancy of microorganisms at the phylum and species taxonomical level from rRNA (i.e., active bacteria or archaea) and rDNA (i.e., all bacteria or archaea) identified using targeted metagenomics were compared. Dormancy was calculated using the following equation: $[1 - (\text{relative recovery of a given phyla or subclass in the rRNA based community} / \text{relative recovery of the same phyla or subclass in the rDNA based community})]$ or $1 - (\text{proportion of active OTUs from a given phyla and subclass})$. This will be represented as $1 - (\text{rRNA/rDNA})$ throughout the paper. It was hypothesized that bacteria and archaea in hypersaline lake communities exhibit lower levels dormancy than bacterial and archaeal communities in geologically similar freshwater lake controls. In addition, we measured a suite of environmental characteristics known to influence microbial community structure, such as pH (i.e., Fierer *et al.*

2005), conductivity (i.e., Hur *et al.* 2011), temperature (i.e., Waldrop 2000, Panswad *et al.* 2003), dissolved oxygen (i.e., Downing *et al.* 2008), nitrogen and phosphorus availability (i.e., Liu *et al.* 2012) and micronutrients (i.e., Viets 1962). It was also hypothesized that microbial dormancy will decrease as salinity increases in the lakes. Last, it was evaluated whether dormancy influenced bacterial and archaeal richness, diversity, and community composition.

2. MATERIALS AND METHODS

2.1 Lake Descriptions

This study examined five hypersaline and five freshwater lakes in the Western United States between 17 May and 23 June 2012. Hypersaline lakes were defined as those having salt concentrations above 3.5% and freshwater lakes acted as controls. The control lakes had similar size, average depth, and geological origin of at least one of the hypersaline lakes so that bacterial and archaeal ecological responses in a range of lake environments could be compared. The five hypersaline lakes included: Great Salt Lake, Spiral Jetty, UT; Great Salt Lake, Antelope Island, UT; Lake Abert, OR; Salton Sea, CA; and Mono Lake, CA, and the five freshwater lakes included: Silverwood Lake, CA; Riffe Lake, WA; Arivaca Lake, AZ; Lilly Lake, CO, and Mormon Lake, ID. Lake locations (i.e., latitude and longitude) and elevations are summarized in Table 1.

2.2 Limnological Methods

Lake samples were collected and water chemistry was determined from the surface mixed-layer approximately 200 m from shore in the limnetic zone and 3 m below the lake surface in the epilimnion. All sampling occurred over a one-month period to minimize any effect of a thermocline or photoperiod on lake microorganisms. Sampling occurred on clear days between 10 am and 1pm with local temperatures always ranging between 76 - 84°C to limit variations in microbial communities induced by weather. Bacteria and archaea were isolated from approximately 2.0-2.5 L of water onto 142 mm 0.2 micron Supor[®] PES membrane disc filters (Pall Life Sciences, Port Washington, New York, USA) using a pressure filtration system (Advantec MFS Inc., Tokyo, Japan). Sample filters were flash-frozen in liquid nitrogen on site

and stored at $-80\text{ }^{\circ}\text{C}$ until processed. The pressure filtration apparatus was autoclaved after each use to prevent sampling biases. Additional lake samples were removed from the same location and tested for salinity, pH, inorganic nitrogen concentrations (i.e., NO_3^- , NH_4^+), and other potential nutrients (i.e., P, Na, Mg, Ca, Cu, Fe, and K). Briefly, salinity was measured with a conductivity bridge (Beckman, Brea, CA, USA); pH was measured with a Thermo Orion Model 410 pH meter (Thermo Scientific, Beverly, MA, USA); nitrate and ammonium colorimetrically using flow injection analysis (LACHAT Instruments, Loveland, CO, USA); and all other nutrients with an Inductively Coupled Plasma Optical Emission Spectrometer (ICP, Thermo Electron Corporation, Franklin, Maryland, USA). Total nitrogen (TN) and dissolved organic carbon (DOC) were measured by oxidation and subsequent chemiluminescence or nondispersive infrared (NDIR) detection, respectively, using a Shimadzu Total Organic Carbon L-Series analyzer equipped with a Total Nitrogen Measurement L-Series unit (Shimadzu, Kyoto, Japan). Dissolved oxygen, temperature, and electrical conductivity were measured *in situ*. Temperature and dissolved oxygen were measured using a YSI EcoSense DO 200 meter (YSI Inc., Yellow Springs, Ohio, USA) and electrical conductivity was measured using an OAKTON EcoTestr EC Low Meter (Oakton Instruments Inc., Vernon Hills, Illinois, USA).

2.3 Bacterial and Archaeal Dormancy

To investigate the effects of extreme environments on bacterial and archaeal dormancy, dormancy from DNA- and RNA-based communities using bar-coded pyrosequencing was calculated. Total genomic lake DNA and RNA was extracted from filter discs using the PowerSoil DNA Isolation Kit and the RNA PowerSoil Total RNA Isolation Kit (MoBio Corporation, Carlsbad, CA, USA). The RNA extraction protocol was modified to maximize

RNA yields in hypersaline lakes by doubling the aliquot of any buffers that contain SDS or a protein precipitation reagent and incubating at room temperature throughout the extraction process, as suggested by the Great Salt Lake Institute (http://www.westminstercollege.edu/great_salt_lake_institute/). Details of the pyrosequencing procedures are described in detail elsewhere (Hamady *et al.*, 2008; Fierer *et al.*, 2009). 16S rDNA and rRNA genes were amplified using the bacterial specific primer set 515F (5'-GTGCCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACVSGGGTATCTAAT-3') with unique 12-nt error correcting Golay barcodes. The forward primer was designed with a Lib-L A Adapter (5'-CCATCTCATCCCTGCGTGTCTCCGACTCAG-3'), a unique barcode, and a GT-linker on the 5' end; and the reverse primer was designed with a Lib-L B Adapter (5'-CCTATCCCCTGTGTGCCTTGGCAGTCTCAG-3') and a GG-linker on the 5' end. Primer details are summarized in Table 3. For the target amplification of rDNA and rDNA, the following thermal cycle conditions were used: an initial denaturation step at 94°C for 3 minutes followed by 35 cycles of denaturation at 94°C for 45 seconds, annealing at 57.5°C for 30 seconds, and a 45 second extension at 72°C for 90 seconds. DNA was amplified with KAPA2G Robust HotStart (KAPA Biosystems, Boston, Massachusetts, USA). To amplify rRNA, a cDNA pool was created using SuperScript III, One-step RT-PCR System with Platinum Taq (Invitrogen Corporation, Carlsbad, California, USA). The amplified DNA and cDNA samples were purified using an Agencourt AMPure XP PCR Purification (Beckman Coulter Inc., Brea, California, USA) and quantified using a Quant-iT™ PicoGreen dsDNA Kit (Invitrogen Corporation, Carlsbad, California, USA) to create approximately equimolar concentrations prior to pyrosequencing. Samples were sequenced at the Brigham Young University DNA Sequencing Center (<http://dnasc.byu.edu/>) in a 454 Life Sciences Genome Sequence FLX instrument (Roche,

Branford, Connecticut, USA). All sequences were analyzed using Mothur open-source, expandable software (http://www.mothur.org/wiki/Main_Page). Only sequences that were > 298 bp in length were included in the analysis to assure the accuracy and quality of pyrosequencing. OTU identification was performed using Megablast at a minimum coverage of 99%, and minimum pairwise identity of 97%. The phylogenetic identities of sequences were aligned against the SILVA database (<http://www.arb-silva.de>). The alignment involved three steps, including: i) template assignment via kmer searching; ii) pairwise alignment with a de-gapped template using Needleman-Wunsch, Gotoh, and blastn algorithms, and; iii) reinserting gaps using the NAST algorithm. Additionally, multiple pipelines within the software allowed for full functionality of NCBI, Dotor, Sons, Treeclimber, S-Libshuff, and Unifrac.

Bacterial and archaeal dormancy was evaluated at the phylum and species levels. To investigate dormancy at the phylum level, the relative recovery of seven major phyla and subclasses of bacteria and two archaeal phyla were determined and dormancy was measured by the following equation: $[1 - (\text{relative recovery of a given phyla or subclass in the rRNA based community} / \text{relative recovery of the same phyla or subclass in the rDNA based community})]$ or $1 - (\text{proportion of active OTUs from a given phyla and subclass})$. This will be represented as 1 - (rRNA/rDNA) throughout the paper. ANOVA (SAS PROC GLM) was used to test for the effect of extreme lake environments on dormancy and relative recovery, and Tukey's HSD test was used to identify significant differences among the hypersaline and freshwater lakes. Also, to evaluate if dormancy structured bacterial and archaeal community structure, a principle coordinate analysis (PCoA) of rDNA and rRNA communities from all lakes was performed. The PCoA used an abundance-based distance matrix that was relativized by individual samples to compensate for any differences in sample amplification during pyrosequencing and included all

78,103 OTUs present in the lakes. The PCoA used BrayCurtus similarity coefficient for the ordination of treatments and the control. Permutational multivariate analysis of variance (PERMANOVA; Aanderud *et al.* 2012; Anderson 2001) was employed to assess the effects of hypersaline and freshwater lake conditions on bacterial and archaeal communities.

PERMANOVA was implemented with the *Adonis* function in the vegan package of the R Statistics Environment (R Development Core Team 2008). To investigate patterns at the species level, a phylogenetic tree of species found in all lakes was created using the Interactive Tree of Life (iTOL) software (<http://itol.embl.de/>), the individual dormancy levels for each OUT were calculated, and bars around the tree to identify a dormancy level of 50% or higher were added. The tree was created with OTUs that possessed at least one rRNA and one rDNA tag sequence. If no rRNA tag sequence was recovered, OTUs possessing at least five rDNA tag sequences were used for the construction of the tree. We focused primarily on bacterial phylogenetics since the archaea primarily fell into two of the four archaeal phyla, and a large portion of taxa were unclassified (13% of total taxa in all samples). Lastly, changes in bacterial OTU richness were quantified using Chao1 estimator and OTU diversity was determined using an Inverse Simpson index among the different lake chemistries (Chao 1984; Aanderud and Lennon 2001) using ANOVA and Tukey's HSD tests.

2.4 Links Between Bacterial and Archaeal Dormancy and Environmental Characteristics

Any relationship between dormancy and lake chemistry was assessed by correlating bacterial community composition and salinity, temperature, dissolved oxygen, total phosphorus, TN, and pH using Redundancy analysis (RDA). The relationships between dormancy and chemistry variables that directly related to the bacterial and archaeal communities were evaluated

using linear regression. The RDA was performed on a relativized data matrix of all rDNA and rRNA OTUs with the *Adonis* function in the *Vegan* package of the R Statistics Environment (R Development Core Team 2008). Regressions were performed with Sigma Plot version 12.5 (Systat Software, San Jose, CA).

3. RESULTS

3.1 Freshwater and Hypersaline Lake Dormancy

Dormancy of bacterial and archaeal taxa were more than 50% lower in hypersaline (HS) than in freshwater (FW) lakes. Based on pyrosequencing of rDNA and rRNA sequences, overall dormancy decreased at least 2-fold in HS compared to FW lakes for both bacteria (ANOVA: hypersaline to freshwater, $F_{(1)}=48$, $P<0.005$) and archaea (ANOVA: hypersaline to freshwater, $F_{(1)}=33$, $P<0.005$, Fig 1). Of the bacterial phyla and subclasses present in the samples, five exhibited strong trends of dormancy in HS lakes. Alphaproteobacteria and Actinobacteria demonstrated at least a two-fold decrease in dormancy levels. Firmicutes, Bacteroidetes, and Gammaproteobacteria, however, each demonstrated at least a seven-fold decrease in dormancy (Fig 2). Together, these three phyla and two subclasses represented 36.2% of all HS-dwelling bacteria and 72.4% of the overall bacterial communities.

The reduction in dormancy in archaeal phyla occurred primarily in the Euryarchaeota (Fig 4). Euryarchaeota were rarely dormant in HS lakes and very abundant, constituting upwards of 65% of the archaeal community. An eight-fold decrease in dormancy by the dominant Euryarchaeota was accompanied by a similar reduction of dormancy levels in Crenarchaeota from FW to HS. The Crenarchaeota phylum represented a smaller component of the archaeal community (22%) in FW and HS lakes.

Three bacterial phyla and one subclass, Cyanobacteria, Verrucomicrobia, Planctomycetes, and Betaproteobacteria, demonstrated a small increase in dormancy in HS lakes. However, these phyla only represented 4.3% and 11.2% of FW and HS lake communities, respectively (Fig 3, 5).

3.2 Dormancy of Individual Species

To visualize the level of dormancy observed in FW and HS lakes at a species level, a phylogenetic tree was constructed and the tree ringed with a predetermined level of dormancy ($X = 1 - (rRNA/rDNA)$). Dormancy for the tree was defined as $X > 0.50$. A higher frequency of dormant species was visible in FW-dwelling bacteria (175.8%) than HS-dwelling counterparts ($F_{(1)} = 48, P < 0.005$) (Fig 6). Of the total representative species on the tree, 408 were dormant in FW and 232 were dormant in HS lakes.

Although a general trend of higher dormancy levels was identified across all species in FW lakes, species in the Firmicutes and Bacteroidetes phyla and Gammaproteobacteria subclass experienced the most extreme differences in dormancy between FW and HS systems. Each showed at least a seven-fold reduction in the number of species dormant in HS lakes compared to FW lakes. Furthermore, of the 109 representative species within Firmicutes, 91 were dormant in FW lakes and only 13 of the 109 species were dormant in HS lakes. Species in the genus *Clostridium* within the phylum Firmicutes were primarily responsible (87% of all Firmicutes) for the high levels of dormancy observed. Of the 556 representative species within Gammaproteobacteria, 93 were dormant in FW lakes and only 14 were dormant in HS lakes. Species within Bacteroidetes did not have discernable patterns of dormancy.

We found other isolated circumstances where a single species determined a majority of the overall dormancy identified in a phylum or subclass. A high concentration of dormancy within one species in HS samples was found in the Chloroflexi and Deinococcus phyla and the Deltaproteobacteria subclass. In all three taxa, one species is responsible for at least 45% of the observed dormancy while the residual dormancy is evenly distributed across the remaining

species. *C. aurantiacus* caused 45.2% of the total observed dormancy within the phylum Chloroflexi, 56.8% within the phylum Deinococcus was caused by *D. radiodurans*, and 62.4% within the subclass Deltaproteobacteria was caused by *D. delicata*.

Species in four minor phyla demonstrated lower dormancy rates in FW lakes compared to HS lakes. In FW lakes, only a single genus of Cyanobacteria, *Prochlorococcus*, was dormant, while 17 of the 25 represented genera were dormant in HS lakes; a difference of 64%. Verrucomicrobia and Planctomycetes had 5 and 3 dormant species in FW lakes and 27 and 15 dormant species in HS lakes, respectively. In both FW and HS lakes, Betaproteobacteria had dormant species in every genus. The only exceptions to this was the genus *Dechloromonas*, where all 23 (100%) of the species were dormant in FW lakes only, and the genus *Aquamonas*, where all 16 (100%) of the species were dormant in FW lakes.

3.3 Bacterial Dormancy and Lake Environmental Characteristics

As expected, bacterial communities in HS and FW lakes were greatly influenced by different environmental characteristics. Based on the redundancy analysis (RDA) plot, all five HS communities were influenced by salinity. FW lake communities were influenced by three different characteristics. One of the FW lake bacterial communities (Lily Lake) was influenced by temperature. The recorded temperature in Lily Lake was 14.9°C; 4.8°C colder than the average of all other sampling sites. Two of the FW communities (Mormon Lake and Silverwood Lake) were influenced by dissolved oxygen concentrations. The recorded dissolved oxygen concentrations of Mormon Lake and Silverwood Lake were 90.7% and 90.4%, respectively. The remaining communities (Arivaca Lake and Riffe Lake) were driven by total phosphorus concentrations. The recorded total phosphorus concentrations were 30.0µg/L and 71.0µg/L,

respectively; ten-times lower than the average total phosphorus concentrations across all other sampling sites. The overall RDA model was significant ($P < 0.005$, $F_{(19)} = 5.27$) (Fig 7).

Significant differences were identified in general lake chemistry characteristics (i.e., pH, salinity, temperature, dissolved oxygen, and mineral concentrations) between HS and FW lakes; lake chemistry is summarized in Table 2. Based on one-way ANOVA results, HS compared to FW lakes had higher salinity, pH, TN, and TP, while FW lakes had higher dissolved oxygen levels. Specifically, electrical conductivity (Ec), a measurement of salinity, was approximately 50,340.0 dS/cm higher in HS lakes compared to FW lakes ($F_{(1)} = 8.46$, $P < 0.005$). TP, another environmental driver, was 1040.0 $\mu\text{g/L}$ higher in HS lakes compared to FW lakes ($F_{(1)} = 3.29$, $P < 0.05$).

Dormancy was predominantly related to phosphorus in FW lakes and salinity in HS lakes. In FW lakes, dormancy decreased with increasing P ($R^2 = 0.88$, $F_{(9)} = 17.6$, $P = 0.015$) but in HS lakes there was no such relationship ($R^2 = 0.01$, $F_{(9)} = 17.014$, $P = 0.916$). In HS lakes, dormancy decreased with increasing salinity ($R^2 = 0.99$, $F_{(9)} = 138.3$, $P < 0.005$) and the trend was also apparent in FW lakes ($R^2 = 0.70$, $F_{(9)} = 7.052$, $P = 0.07$) albeit, less significant than the analogous trend for phosphorus (Fig 8, 9).

4. DISCUSSION

4.1 Overall Dormancy

Changes in environmental conditions cause species to adapt to and occupy different niches to reduce out-competition. Although natural selection is typically viewed as an evolutionary process to attaining a higher species diversity, we see a different trend in extreme environments. Because extreme environments are naturally nutrient-poor and have an strong extreme environmental driver, microbial populations reach an evolutionary “straight-jacket;” where they are forced into evolving life history strategies that allow them to cope with the predominant extreme variable. As hypothesized, bacteria and archaea exhibited lower levels dormancy in extreme lake environments compared to bacterial and archaeal communities in freshwater lake environments. Further, as hypothesized, microbial dormancy decreased as the dominant extreme environmental variable (i.e., salinity) increased in the lakes. Stated plainly, bacteria and archaea in hypersaline lakes have evolved to contend predominantly with salinity and are more active in these environments as salinity overshadows any other variations in the environment. This potentially creates niches and modulates microbial activity and dormancy. As the overarching extreme stress decreases so does the importance of microorganisms to adjust to an extreme environment. This infers that different levels of extreme evolutionary drivers (i.e., nutrient fluctuations, energy availability, gradients, etc.) will cause changes in life history strategies for some, but not all microorganisms. The data presented here suggest that microbial dormancy occurs along a gradient and is linearly-dependent. When an extreme environmental driver is sufficiently high, however, the data plateau, suggesting that there are limits to a microbial population’s dormancy levels. Because bacterial dormancy and relative recoveries

were statistically similar to those of archaeal communities, the remainder of the analyses will be discussed in terms of bacterial communities only.

4.2 Species' Dormancy and Life History Strategies

Dormancy was examined at the phylum and species levels by evaluating the 3,021 FW- and HS-dwelling bacteria with the Interactive Tree of Life (iTOL). That approximately 175% higher dormancy was observed in freshwater systems compared to hypersaline systems was astounding and tends to differ from previous hypotheses of dormancy in extreme environments (Sussman 1973, DelGiorgio *et al.* 1995). It was generally thought that dormancy was a life history strategy for any microorganism in an extreme environment. However it appears that, at least in hypersaline lake environments, dormancy is not widely used as a life history strategy for a majority of microorganisms.

Species of genus *Clostridium* (phylum Firmicutes) were primarily responsible (87% of all Firmicutes) for the observed dormancy in freshwater systems. Since the clostridia are strictly obligate anaerobes and high levels of dissolved oxygen were detected in the freshwater lakes that were sampled (table 2), widespread dormancy within this phylum can be expected. Another interesting example was the genus *Dechloromonas* within the subclass Betaproteobacteria, where all 23 (100%) of the species were dormant in freshwater samples. The species within the genus *Dechloromonas* are known to thrive in environments with low levels of ammonium (Mouser *et al.* 2009); however, ammonium levels in all five freshwater lakes sampled for this study were below detection levels. Undetectable concentrations of ammonium can be responsible for the sudden increase in dormancy levels in the genus *Dechloromonas* in freshwater systems.

Why such high levels of dormancy were identified in hypersaline-dwelling Cyanobacteria, Verrucomicrobia, Planctomycetes, and Betaproteobacteria is unclear. Recent studies suggest that this may be due to the fact that unvarying environmental conditions (i.e., hypersaline lakes) favor microorganisms with a narrow functional repertoire of genes (specialists) – which many Cyanobacteria, Verrucomicrobia, Planctomycetes, and Betaproteobacteria are not (Parnell *et al.* 2010). However, each of these phyla and subclasses have been shown to survive in saline lake environments (Chatchawan *et al.* 2010). It is interesting to note that although these four phyla survive in hypersaline environments, none the saline environments previously evaluated exceeded a salinity of 3.7% (Salcher 2008, Chatchawan *et al.* 2010). By comparison, the hypersaline lakes in this study, had salinities ranging from 3.72-33.50%.

Microorganisms in extreme environments have evolved a different life history strategy to cope with environmental pressures. It is a possibility that when an extreme environment constricts a microbial community, there might be an increased rate of microevolution events to allow for a greater chance of adapting to the extreme environment. If microorganisms were to simply use a dormancy life history strategy in an extreme environment such as a hypersaline lake, energy storage would soon be depleted with no hope of finding a more habitable area. A majority of microorganisms in hypersaline lakes have life history strategies that include: a reduced number of thymines (a UV “target”), colorful carotenoids to allow for photoprotection, compact surface proteins and the ability to increase osmolarity in the cytoplasm to prevent any loss of water to the external environment.

4.3 Phosphorus and Salinity Environmental Drivers

While phosphorus has been demonstrated to influence dormancy on a continual scale by Jones *et al.* (2010), we identified a similar characteristic when examining the effect of salinity. The correlation of dormancy salinity across each of the ten lakes demonstrated that salinity, more so than total phosphorus concentration, was driving the rates of dormancy in hypersaline lakes. Because phosphorus is essential for creating nucleotides and ATP, it is understandable why higher levels of total phosphorus correlates to lower levels of dormancy; the phosphorus is providing the necessary building blocks for microorganisms to constantly survive and persist. As previously suggested, the findings of this study show that phosphorus is strongly correlated to dormancy in moderate environments, however, when salinity is a prominent environmental driver in the system, the extremity of the environmental driver overshadows the nutrient as a determining factor for dormancy.

Salinity may override phosphorus and other lake chemistry characteristics as a determining factor for dormancy because the high levels of salinity create a more stable environment. The salinity is so omnipresent in the environment that the microbial community is no longer affected by different micro-niches; rather, once a microorganism has evolved to cope with the osmotic stress, it is able to survive, persist, and evolve in an environment that primarily consists of one niche –salinity.

4.4 Niche Differentiation in Hypersaline Lakes

While microbial environments are relatively confined in most of the biosphere, lake environments diminish the effects of a defined environment. In lakes, Brownian diffusion alone would allow a 0.4 μ m-diameter cell to explore 4.5×10^{-5} μ l of seawater in 10 minutes and 0.08 μ l (~430 μ m cube) in a day (Stocker 2012). Although this would appear to be relatively small on a

macro-scale, on a micro-scale, a 0.4 μ m-diameter cell would potentially come in contact with millions of microorganisms and experience a number of different microenvironments. This explains niche differentiation even at a microbial level in aquatic environments. Although some niche differentiation is known to take place in extreme environments (Fiser *et al.* 2012) the extent to which it took place was unclear.

Extreme environments naturally have a reduction in the number of available niches because they are inherently nutrient-poor. Subsequently, the extremophiles that exist in this environment will be forced to cohabitate many of the same niches (Fiser *et al.* 2012, Oren 2002). It is likely that an extreme variable can limit niche differentiation. If it's salinity in hypersaline lakes or UV in the Atacama Desert, the effect that an extreme environmental driver has on the available niches could override the obligation for total niche differentiation (Jones *et al.* 2010, Sexton *et al.* 2009). Extremophile microbial communities may be swayed more by the dominant environmental driver than the evolutionary need to locate an ideal niche.

The combination of fewer niches and a more stable environment from the extreme salinity may decrease biodiversity and increase the representation of rare taxa in hypersaline lakes. A recent study about subterranean amphipod communities found in extreme, energy-poor environments demonstrated reductions in diversification of the communities (Fiser *et al.* 2012). The data presented here suggest that, like these amphipod communities, microbial communities in hypersaline lakes do not follow a fully niche-based evolutionary mechanism, nor do they follow a fully neutral evolutionary mechanism; rather, they are undergoing an evolutionary mechanism that incorporates aspects from both neutral- and niche-based theories.

4.5 Conclusion

The practical application and ecological implication of this study demonstrates the importance of microbial dormancy in extreme environments. It is concluded that microorganisms in hypersaline lake environments exhibit reduced microbial dormancy and that dormancy decreases as the extreme environmental driver increases. Additionally, salinity, as opposed to phosphorus, is the predominant factor determining dormancy levels in hypersaline environments.

These findings invite many more questions. Although hypersaline lakes were used to represent an extreme environment, perhaps other extreme environments such as, geothermal springs, polar lakes, desert soils, and alkaline lakes would show similar trends. Because salinity is a strong environmental driver, perhaps a lake with extreme fluctuations in water elevation or a lake that experiences a robust spring runoff would show different dormancy trends throughout the year. It might also be interesting to study systems that have more than one extreme environmental driver to understand how drivers interact with their environment to cause different trends in microbial dormancy. Great Salt Lake is an ideal system to examine other hypotheses because of the large annual fluctuations in salinity and temperature.

As research in the field of microbial dormancy broadens, important questions about biodiversity, possible industrial and agricultural applications, and even microbial macroecology will be answered.

TABLES AND FIGURES

Table 1. Locations and elevations of freshwater and hypersaline lakes

<i>Sample</i>	<i>Elevation (m)</i>	<i>Location</i>
Great Salt Lake, Spiral Jetty, UT	1285	N 41°25.944' W 112°39.777'
Great Salt Lake, Antelope Island, UT	1280	N 41°03.641' W 112°14.668'
Salton Sea, CA	-77	N 33°26.591' W 115°50.952'
Lake Abert, OR	1287	N 42°37.554' W 120°11.191'
Mono Lake, CA	1948	N 37°56.663' W 119°01.048'
Mormon Lake, ID	1542	N 43°16.007' W 114°50.181'
Riffe Lake, WA	249	N 46°29.261' W 122°11.228'
Arivaca Lake, AZ	1153	N 31°31.802' W 111°15.137'
Lily Lake, CO	2728	N 40°18.477' W 105°32.521'
Silverwood Lake, CA	1020	N 34°17.122' W 117°20.523'

Table 2. Environmental characteristics of hypersaline and freshwater lakes

	<i>Freshwater lakes</i>	<i>Hypersaline lakes</i>	<i>P-values</i>
Chemical Characteristics			
pH	7.00 ± 0.18	8.71 ± 0.47 *	0.0960
Dissolved O ₂ (%)	92.38 ± 1.37	71.22 ± 3.49 **	0.0050
Temperature (°C)	17.98 ± 1.40	20.46 ± 2.11	0.3576
Ec (dS/cm)	4.10 ± 2.45	50,435 ± 32,184 ***	0.0005
SAR (mg/L)	0.22 ± 0.07	4.79 ± 3.52	0.2303
Nutrients			
N-NH ₄ ⁺ (mg/L)	ND	1.15 ± 0.44 *	0.0327
N-NO ₃ ⁻ (mg/L)	0.26 ± 0.06	0.18 ± 0.06	0.3757
Total N (µg/L)	2420.17 ± 242.13	7800.90 ± 119.08 **	0.0022
Total P (µg/L)	128.20 ± 39.22	1168.80 ± 453.82 *	0.0417
DOC (mg/L)	3.98 ± 1.97	0.93 ± 0.24	0.1206
Macronutrients			
K (mg/L)	32.72 ± 9.07	2079.10 ± 1051.03	0.0874
Ca ²⁺ (mg/L)	30.29 ± 7.32	343.78 ± 144.41	0.0621
Mg ²⁺ (mg/L)	18.53 ± 7.63	328.17 ± 129.93	0.1433
Na ⁺ (mg/L)	184.12 ± 45.28	4423.36 ± 1143.44 ***	0.0004

Data (mean ± SEM) are based on totals from all lake samples. Asterisks indicate significant differences between samples (* = P 0.05-0.01, ** = P 0.01-0.001, *** = P < 0.001) based on one-way ANOVA results.

Table 3. PCR and RT-PCR primers and barcodes for freshwater and hypersaline lake pyrosequencing

<i>Sample</i>	<i>Sample Type</i>	<i>Forward Primers (Lib-L-AdapterA=30bp; Barcode=12bp; GT-Linker; 515F Primer=19bp)</i>
Great Salt Lake, Spiral Jetty	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGGACGCACTGT GT GTGCCAGCMGCCGCGGTAA
Great Salt Lake, Antelope Island	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AACTGTTCATG GT GTGCCAGCMGCCGCGGTAA
Salton Sea	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACTCACGGTATG GT GTGCCAGCMGCCGCGGTAA
Lake Abert	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACAGACCACTCA GT GTGCCAGCMGCCGCGGTAA
Mono Lake	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGCAGAGCCTA GT GTGCCAGCMGCCGCGGTAA
Mormon Lake	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGACCGTCAGAC GT GTGCCAGCMGCCGCGGTAA
Riffe Lake	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGCTTGACAGCT GT GTGCCAGCMGCCGCGGTAA
Arivaca Lake	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACGCTCATGGAT GT GTGCCAGCMGCCGCGGTAA
Lily Lake	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACCAGACGATGC GT GTGCCAGCMGCCGCGGTAA
Silverwood Lake	DNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACCAGCGACTAG GT GTGCCAGCMGCCGCGGTAA
Great Salt Lake, Spiral Jetty	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGCCATACTGAC GT GTGCCAGCMGCCGCGGTAA
Great Salt Lake, Antelope Island	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AAGAGATGTCGA GT GTGCCAGCMGCCGCGGTAA
Salton Sea	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACTCGCACAGGA GT GTGCCAGCMGCCGCGGTAA
Lake Abert	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGGCTACACGAC GT GTGCCAGCMGCCGCGGTAA
Mono Lake	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AAGCTGCAGTCG GT GTGCCAGCMGCCGCGGTAA
Mormon Lake	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACAGTAGCTTG GT GTGCCAGCMGCCGCGGTAA
Riffe Lake	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGAGAGCAAGTG GT GTGCCAGCMGCCGCGGTAA
Arivaca Lake	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACGTACTCAGTG GT GTGCCAGCMGCCGCGGTAA
Lily Lake	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG ACAGCAGTGTC GT GTGCCAGCMGCCGCGGTAA
Silverwood Lake	cDNA	CCATCTCATCCCTGCGTGTCTCCGACTCAG AGCATATGAGAG GT GTGCCAGCMGCCGCGGTAA
		<i>Reverse Primer (Lib-L-AdapterB=30bp; GG-Linker; 806R Primer=20bp)</i>
All Samples	DNA/cDNA	CCTATCCCCTGTGTGCCCTTGGCAGTCTCAG GG GGACTIONVSGGGTATCTAAT

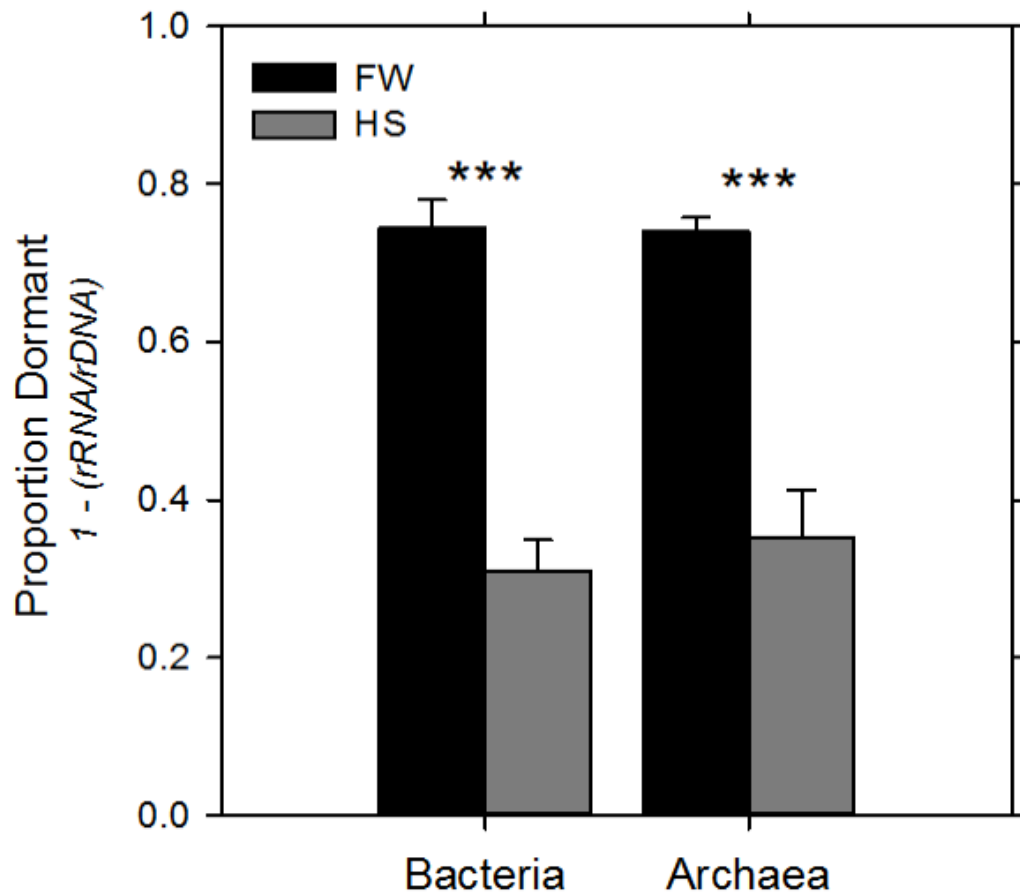


Figure 1. Bacterial and archaeal dormancy in freshwater (FW) and hypersaline (HS) lakes. Dormancy is calculated as 1-(relative recovery of a given phyla or subclass in the rRNA based community / relative recovery of the same phyla or subclass in the rDNA based community) ($1 - (rRNA/rDNA)$). Data (mean \pm SEM) are based on operational taxonomic units (OTU) using 97% similarity cut-offs from 16S pyrosequence libraries. Asterisks indicate significant differences between treatments (* = P 0.05-0.01, ** = P 0.01-0.001, *** = P < 0.001) based on ANOVA.

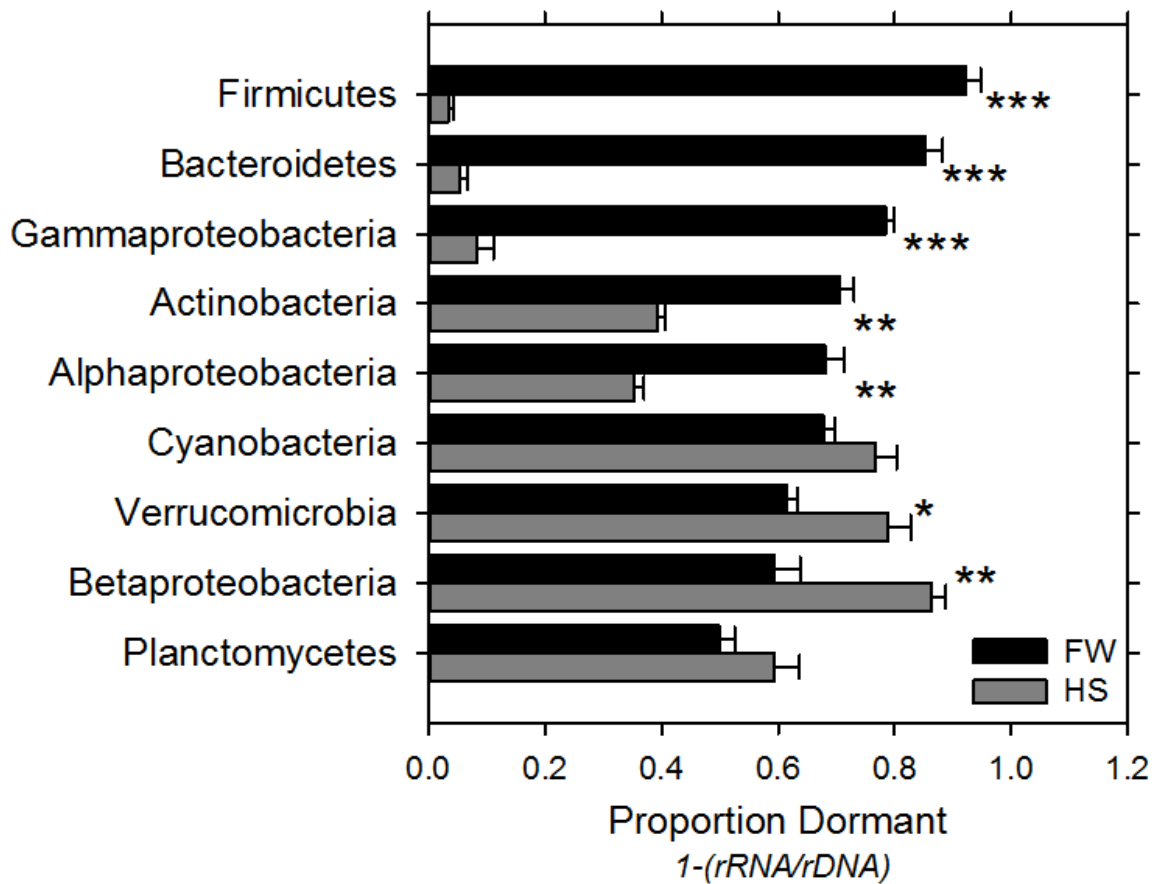


Figure 2. Dormancy of nine of the most highly represented bacterial taxa (i.e., five bacterial phyla and three proteobacterial subclasses) in freshwater (FW) and hypersaline (HS) lakes. Each phyla represents at least 1% of the total bacterial community. Data (mean \pm SEM) are based on operational taxonomic units (OTU) using 97% similarity cut-offs from 16S pyrosequence libraries. Asterisks indicate significant differences between treatments (* = P 0.05-0.01, ** = P 0.01-0.001, *** = P < 0.001) based on ANOVA.

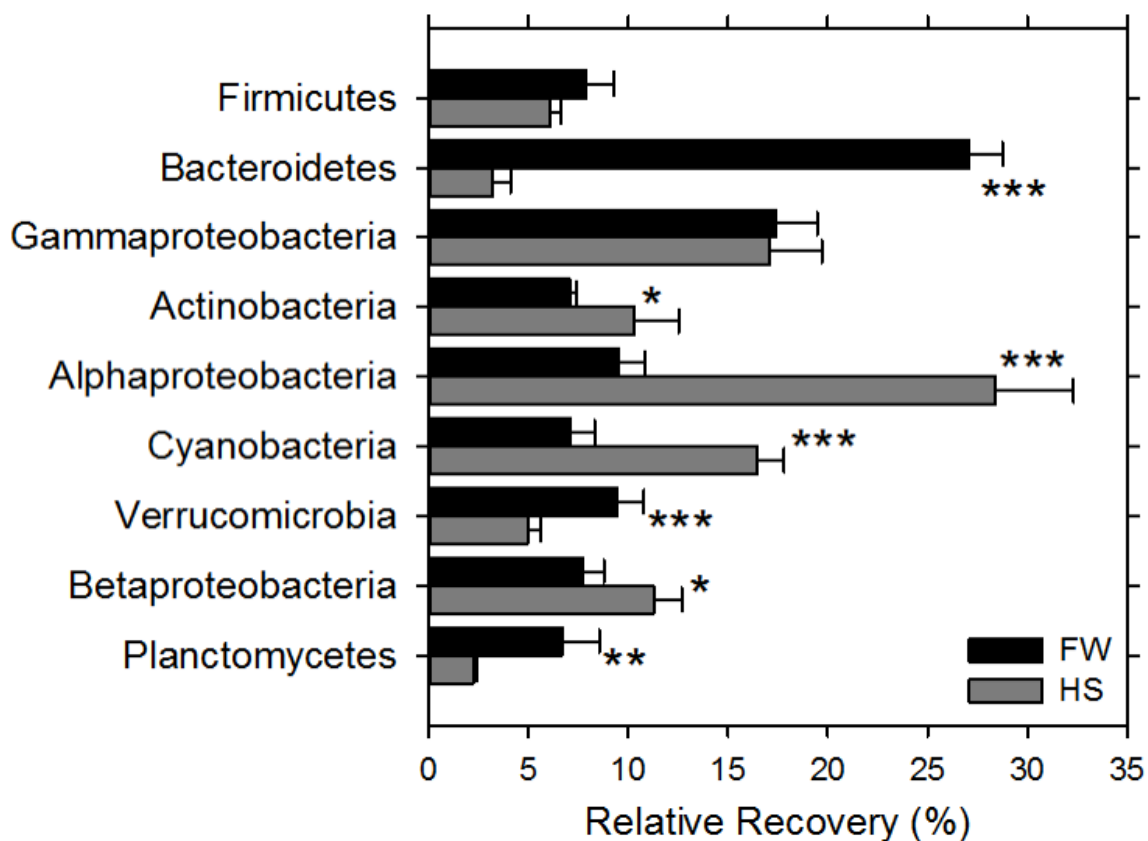


Figure 3. Differences in the relative recovery of the most highly represented bacterial taxa (i.e., five bacterial phyla and three proteobacterial subclasses) from freshwater (FW) and hypersaline (HS) lakes. Recovery is based on the OTUs from 16S rRNA gene copies from pyrosequencing data. Data (mean \pm SEM) are based on operational taxonomic units (OTU) and asterisks indicate significant differences between treatments (* = P 0.05-0.01, ** = P 0.01-0.001, *** = P < 0.001) based on ANOVA.

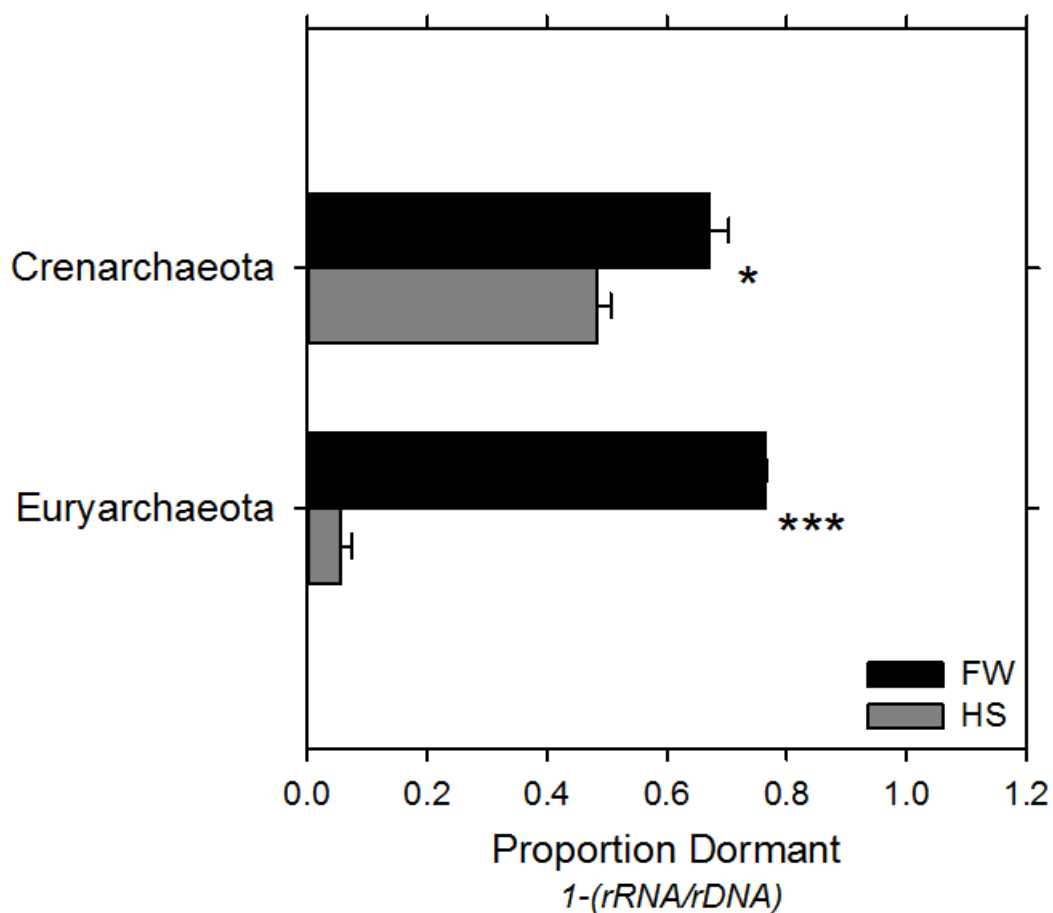
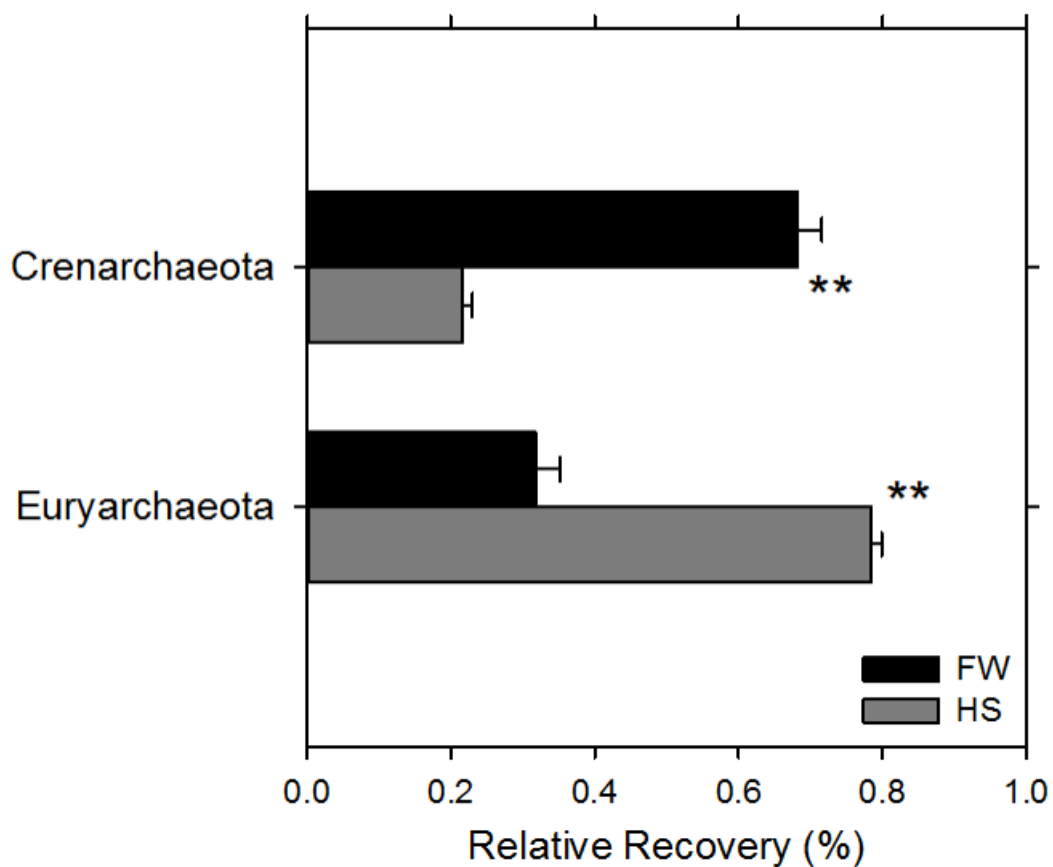


Figure 4. The dormancy of the two archaeal phyla in freshwater (FW) and hypersaline (HS) lakes. Dormancy was calculated as discussed in Figure 2. Data (mean \pm SEM) are based on operational taxonomic units (OTU) using 97% similarity cut-offs from 16S pyrosequence libraries. Asterisks indicate significant differences between treatments (* = P 0.05-0.01, ** = P 0.01-0.001, *** = P < 0.001) based on ANOVA.



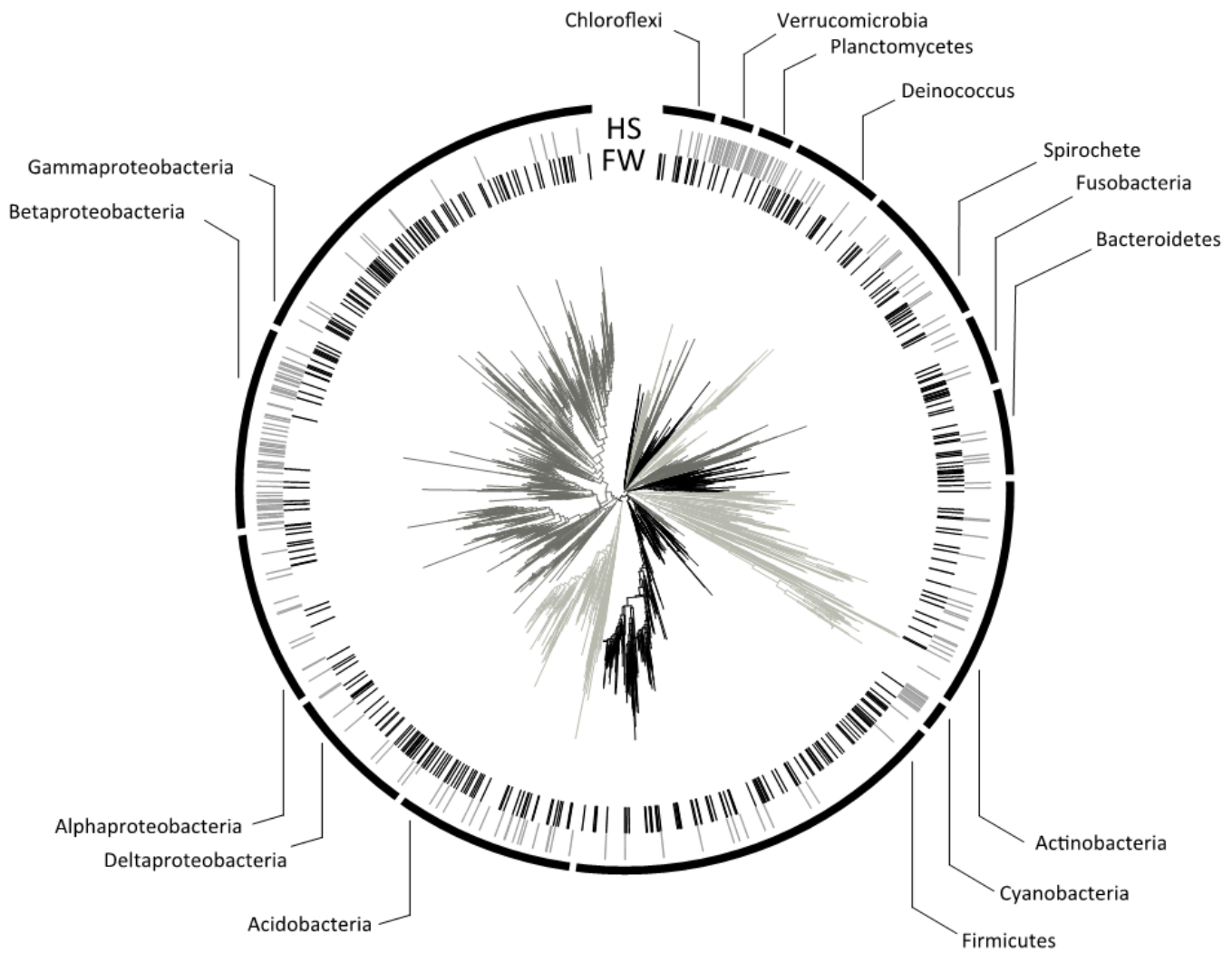


Figure 6. Phylogenetic tree and bar chart representing the dormancy levels of bacterial species in freshwater and hypersaline lake samples. The bars on the perimeter of the tree denote dormant species. Each mark represents dormancy higher than 50% and is specific to a single species on the tree. The inner ring distinguishes all species with dormancy higher than 50% in freshwater (FW) lakes. The outer ring distinguishes all species with dormancy higher than 50% in hypersaline (HS) lakes. (www.itol.embl.de).

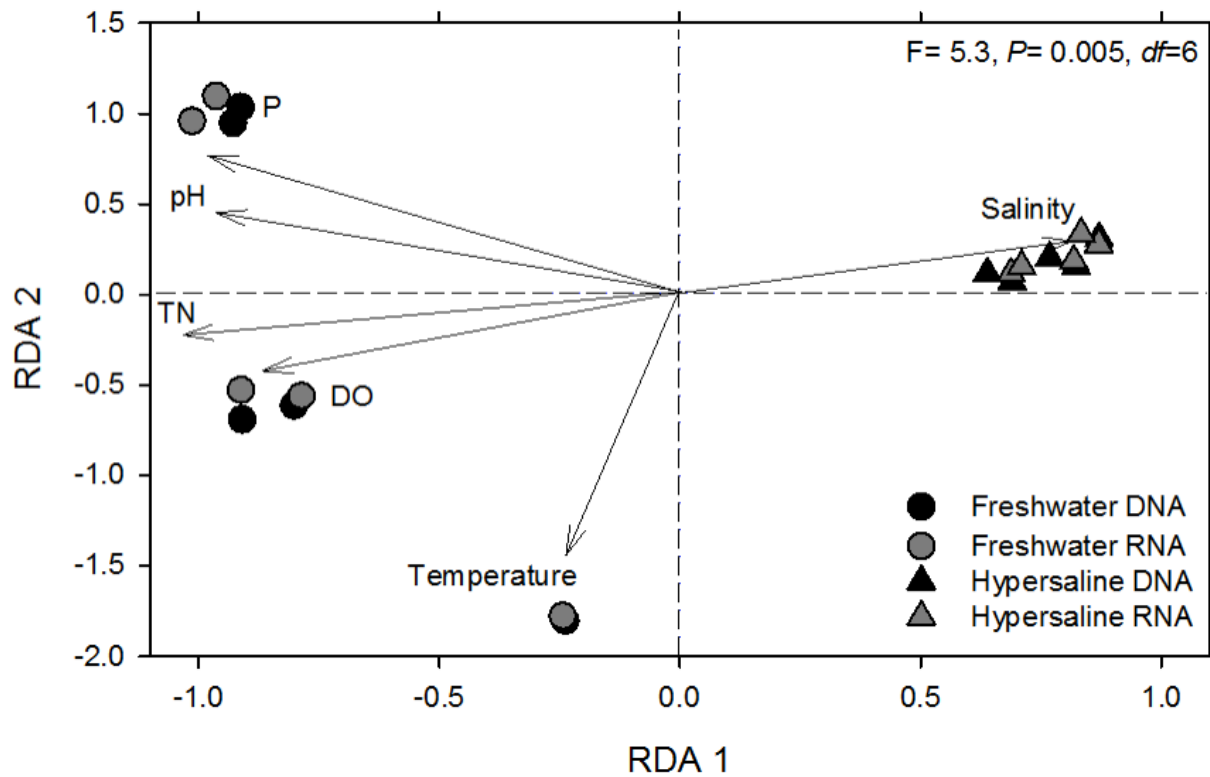


Figure 7. The relationship of bacterial communities and the lake environments using redundancy analysis. The communities plot depicting the variation of species composition in all lake samples. The six environmental variables include: Phosphorus (P), pH, total nitrogen (TN), dissolved oxygen (DO), temperature, and salinity.

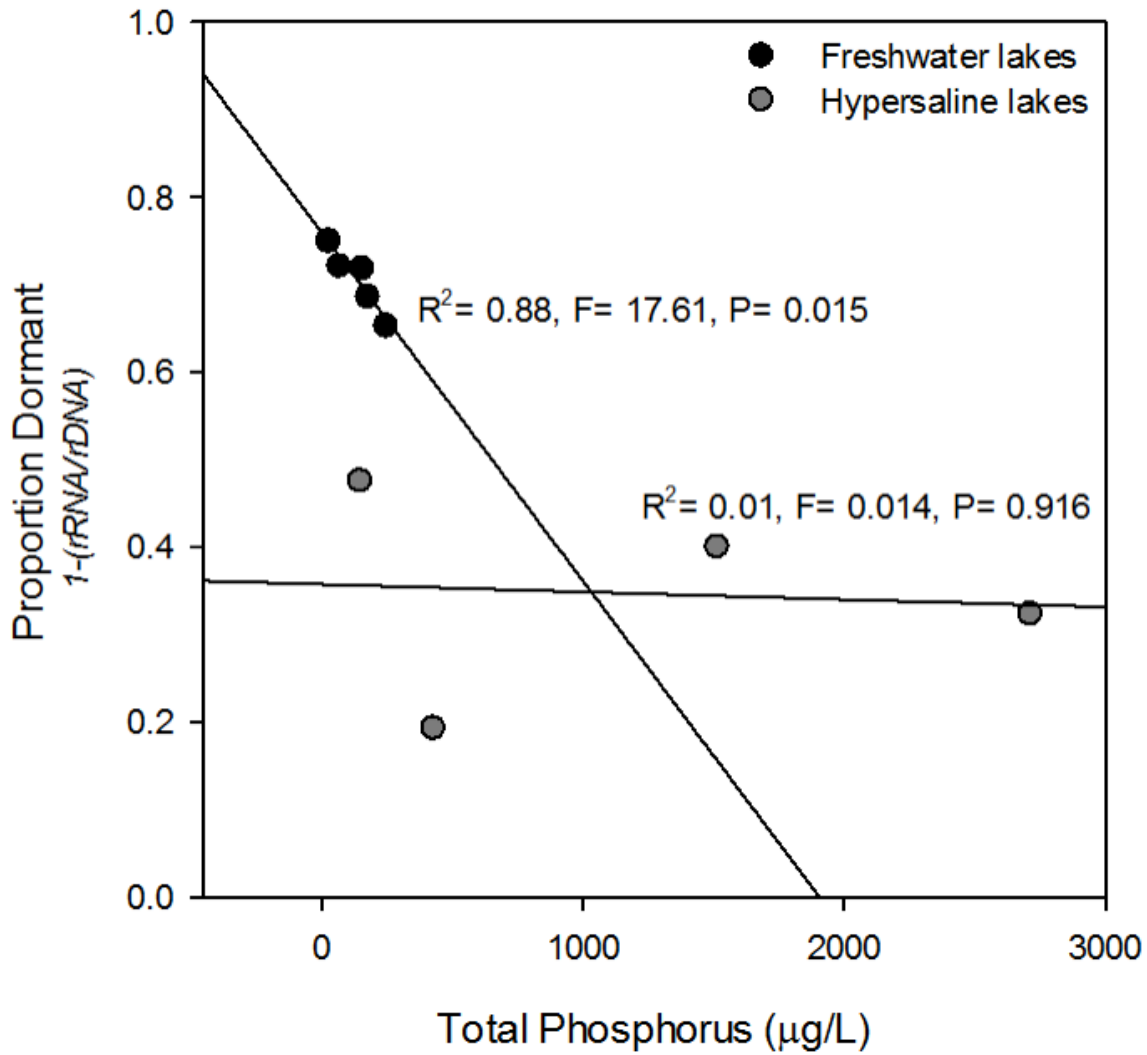


Figure 8. Linear regressions of dormancy as a function of total phosphorus concentrations in freshwater (FW) and hypersaline (HS) lakes.

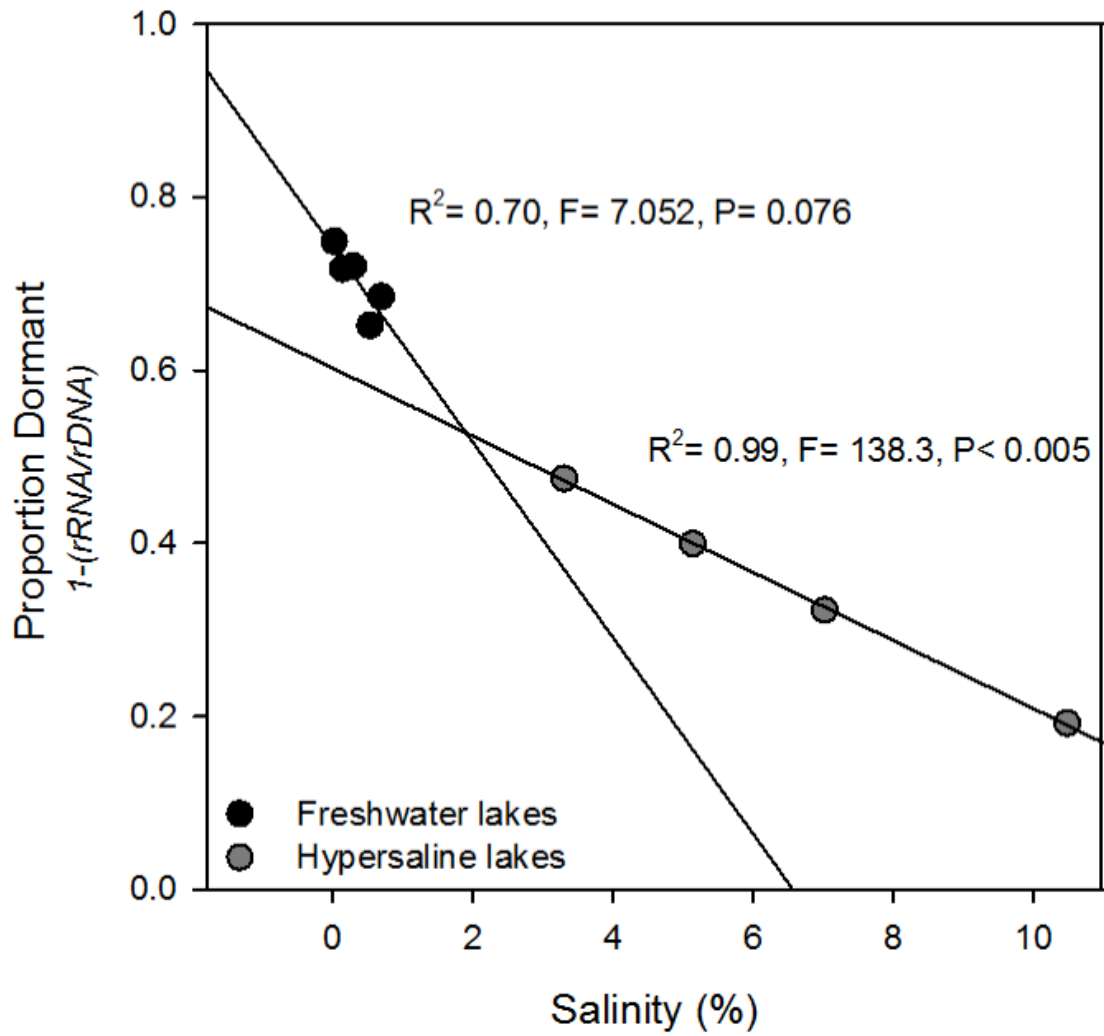


Figure 9. Linear regressions of dormancy as a function of salinity in freshwater (FW) and hypersaline (HS) lakes.

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APPENDIX A

Table S1. Environmental characteristics of hypersaline and freshwater lakes

<i>Sample</i>	<i>pH</i>	<i>EC dS/cm</i>	<i>Ca²⁺ mg/L</i>	<i>Mg²⁺ mg/L</i>	<i>Na⁺ mg/L</i>
Great Salt Lake, Spiral Jetty	7.49	155000	565.00	565.00	6865.00
Great Salt Lake, Antelope Island	8.24	97000	427.10	427.10	3321.00
Salton Sea	8.17	50.00	711.50	610.90	516.40
Lake Abert	9.83	64.50	6.26	1.40	6160.00
Mono Lake	9.81	60.00	9.05	36.49	5254.40
Mormon Lake	6.91	13.00	19.78	5.88	260.30
Riffe Lake	6.83	0.39	15.30	28.35	167.90
Arivaca Lake	7.11	0.19	21.30	3.88	17.70
Lily Lake	6.56	1.31	42.09	10.84	265.40
Silverwood Lake	7.61	5.50	53.02	43.75	209.30

<i>Sample</i>	<i>SAR mg/L</i>	<i>TP ug/L</i>	<i>TN ug/L</i>	<i>NO₃⁻-N mg/L</i>	<i>NH₄⁺-N mg/L</i>	<i>Cu mg/L</i>
Great Salt Lake, Spiral Jetty	0.06	1030.00	12480.00	0.00	0.80	0.85
Great Salt Lake, Antelope Island	0.07	430.00	5890.00	0.10	0.09	0.06
Salton Sea	0.11	150.00	6430.00	0.34	0.48	0.01
Lake Abert	18.27	2716.00	7360.00	0.22	1.96	0.01
Mono Lake	5.47	1518.00	6840.00	0.23	2.43	0.01
Mormon Lake	0.42	180.00	2550.00	0.16	0.00	0.00
Riffe Lake	0.18	71.00	1950.00	0.19	0.00	0.00
Arivaca Lake	0.03	30.00	3290.00	0.22	0.00	0.01
Lily Lake	0.30	250.00	2170.00	0.21	0.00	0.00
Silverwood Lake	0.16	110.00	2120.00	0.52	0.00	0.00

<i>Sample</i>	<i>Fe mg/L</i>	<i>K mg/L</i>	<i>Mn mg/L</i>	<i>Dissolved O2 (%)</i>	<i>Temperature (°C)</i>
Great Salt Lake, Spiral Jetty	0.13	5930.00	0.63	71.90	18.70
Great Salt Lake, Antelope Island	0.39	2694.50	0.09	77.60	18.40
Salton Sea	0.00	217.20	0.03	78.70	28.90
Lake Abert	0.06	662.90	0.01	59.40	17.60
Mono Lake	0.15	890.90	0.03	68.50	18.70
Mormon Lake	0.18	67.27	0.01	90.70	18.20
Riffe Lake	0.01	26.61	0.00	94.20	14.70
Arivaca Lake	0.12	18.15	0.01	96.90	21.30
Lily Lake	0.05	33.16	0.01	89.70	14.90
Silverwood Lake	0.01	18.44	0.00	90.40	20.80

APPENDIX B

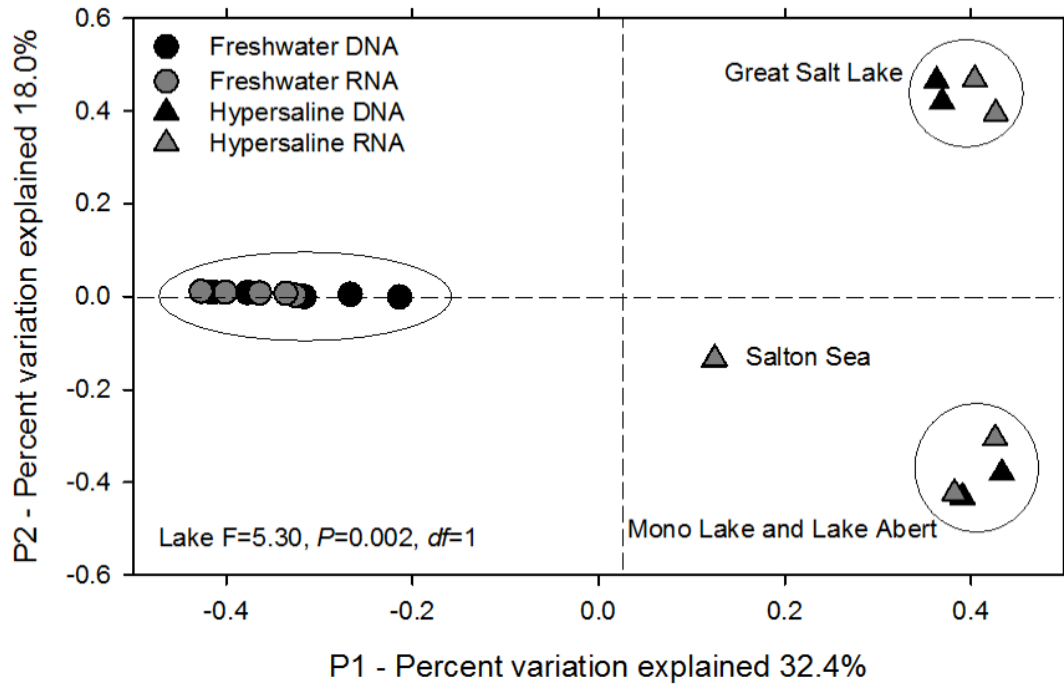


Figure S1. Principle component analysis (PCoA) plot of bacterial species composition in freshwater and hypersaline lake samples. Data are based on operational taxonomic units (OTU) using 97% similarity cut-offs from 16S pyrosequence libraries.

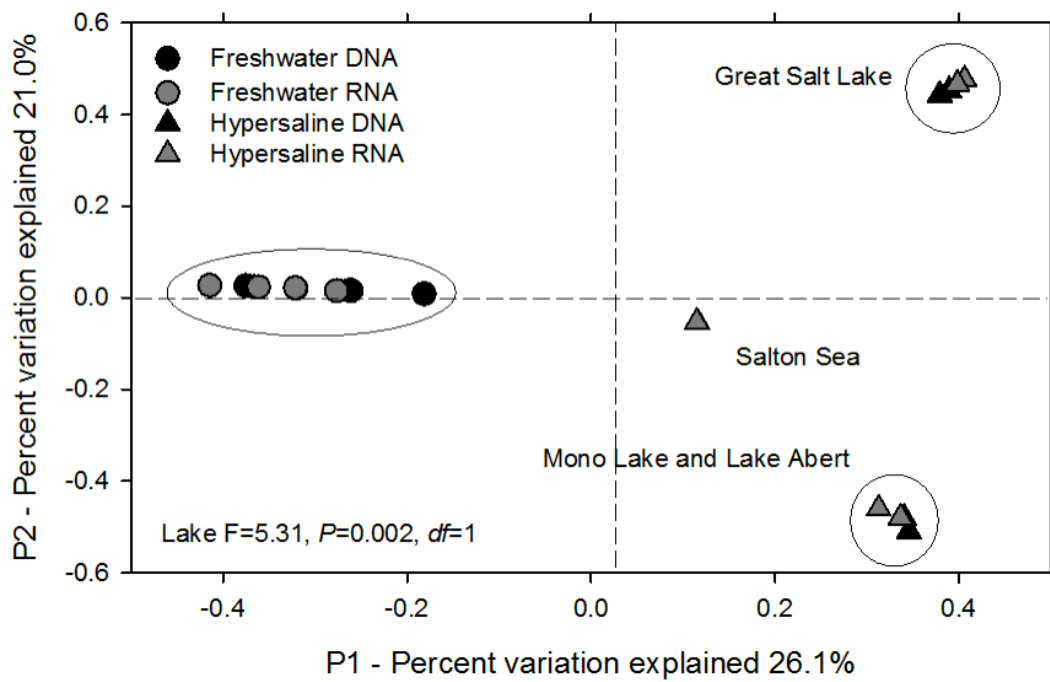


Figure S2. Principle component analysis (PCoA) plot of archaeal species composition in freshwater and hypersaline lake samples. Data are based on operational taxonomic units (OTU) using 97% similarity cut-offs from 16S pyrosequence libraries.

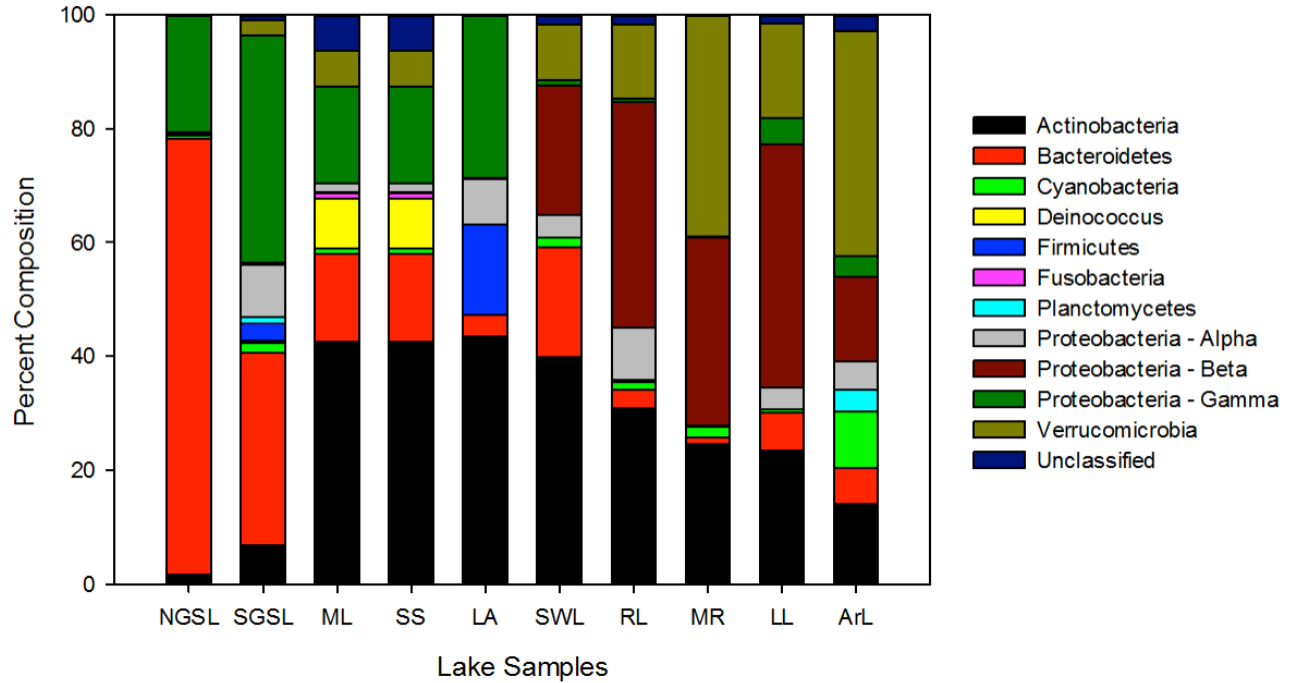


Figure S3. Microbial RNA-based community composition of freshwater (SWL= Silverwood Lake; RL= Riffe Lake; MR= Mormon Lake; LL= Lily Lake; ArL= Arivaca Lake) and hypersaline (NGSL= Great Salt Lake, Spiral Jetty; SGSL= Great Salt Lake, Antelope Island; ML= Mono Lake; SS= Salton Sea; LA= Lake Abert) lake samples. Percent composition was calculated by relativizing the rDNA and rRNA tag sequences of the most highly represented 1000 operational taxonomic units (OTU) across each sample.

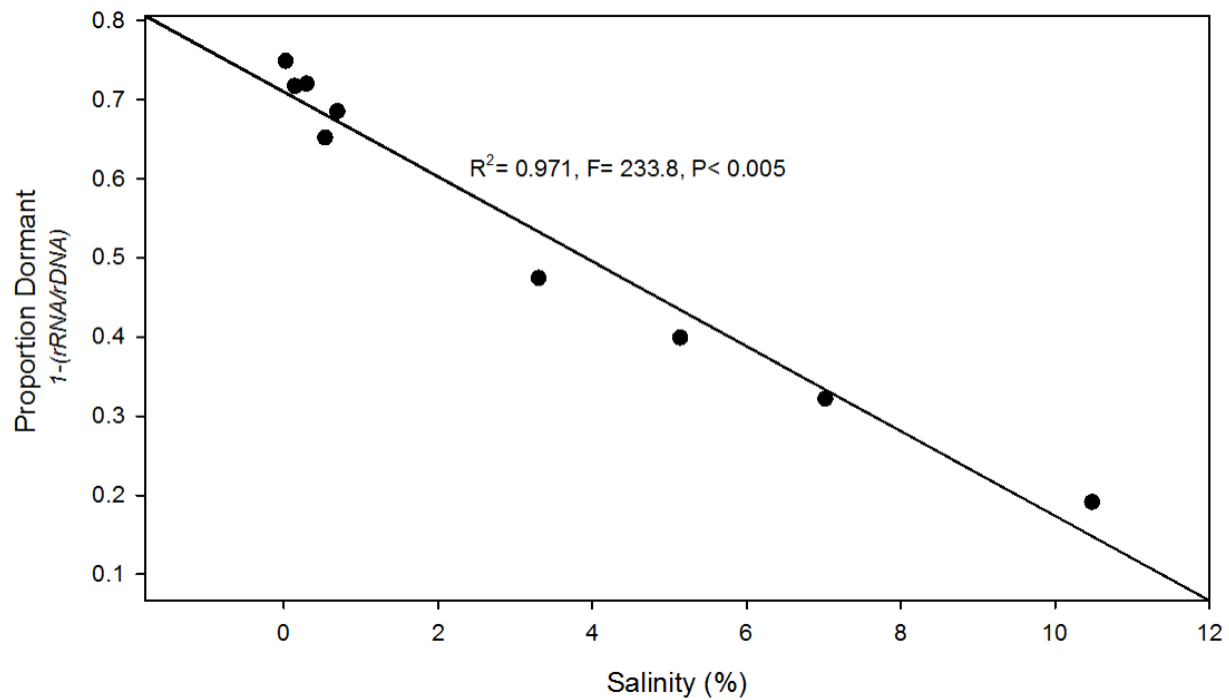


Figure S4. Linear regression of microbial dormancy for all lake samples plotted as function of salinity. Dormancy is calculated as 1-(relative recovery of a given phyla or subclass in the rRNA based community / relative recovery of the same phyla or subclass in the rDNA based community) (1-(rRNA/rDNA)).

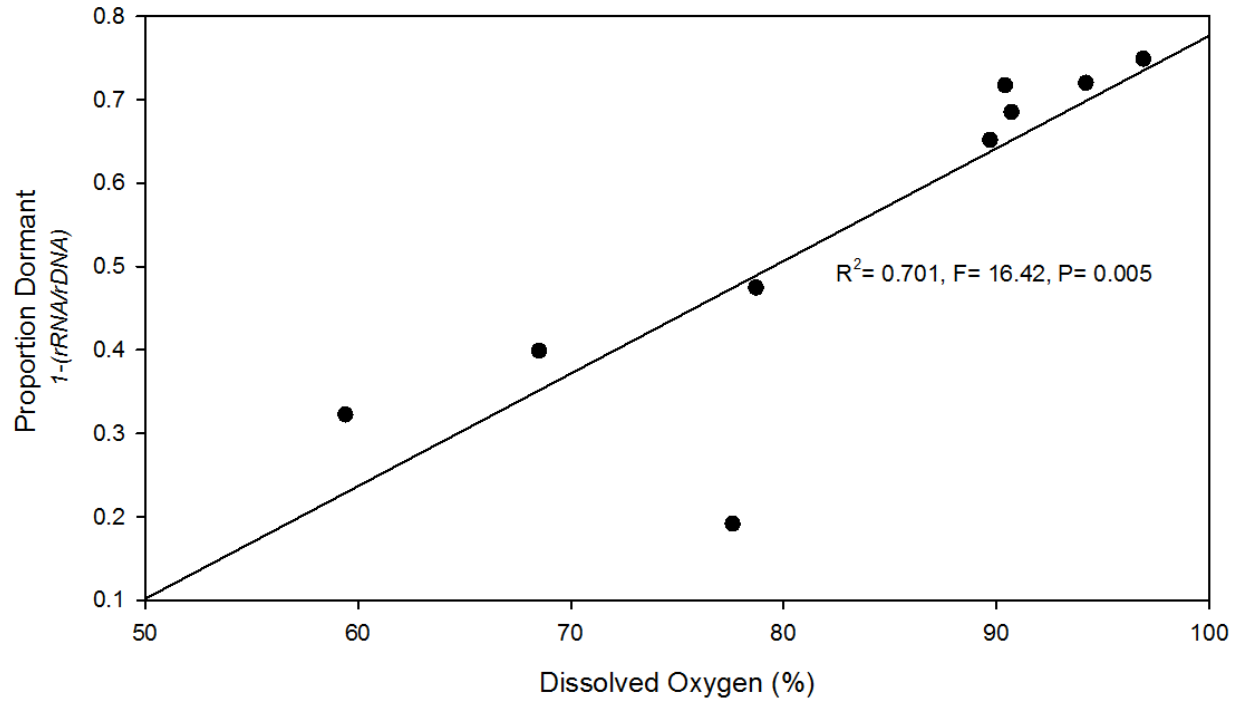


Figure S5. Linear regression of microbial dormancy for all lake samples plotted as function of dissolved oxygen concentrations. Dormancy is calculated as 1-(relative recovery of a given phyla or subclass in the rRNA based community / relative recovery of the same phyla or subclass in the rDNA based community) (1-(rRNA/rDNA)).

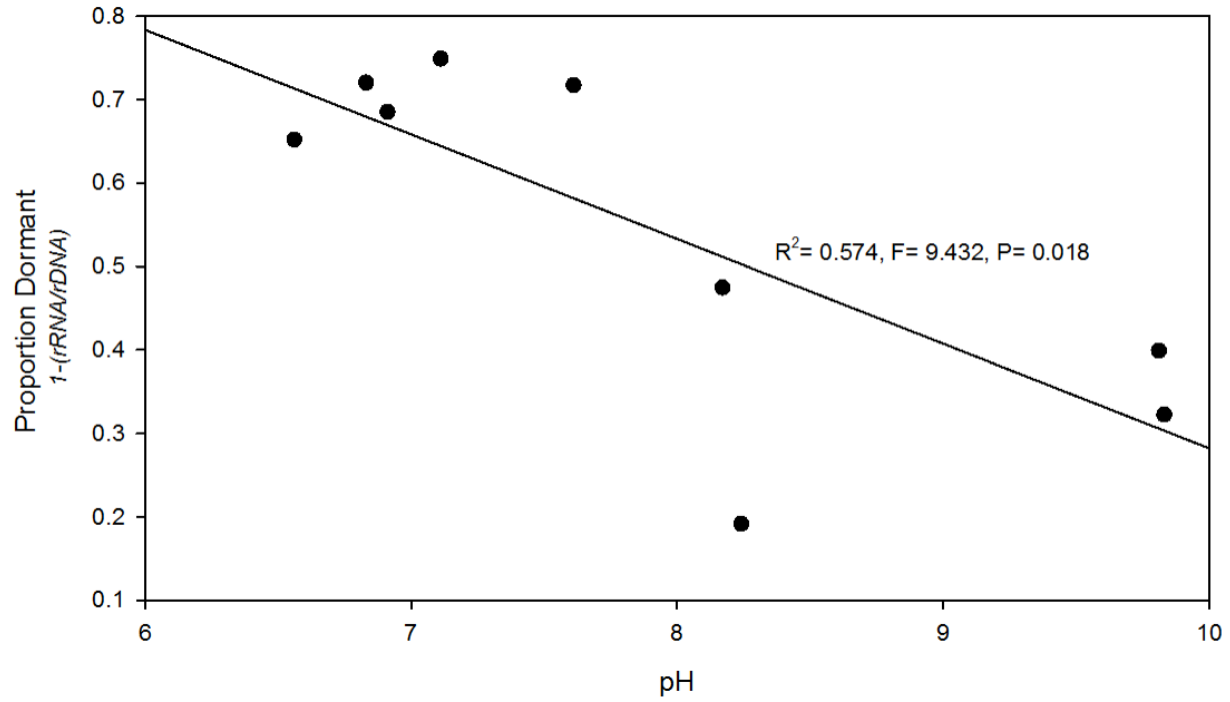


Figure S6. Linear regression of microbial dormancy for all lake samples plotted as function of pH. Dormancy is calculated as 1-(relative recovery of a given phyla or subclass in the rRNA based community / relative recovery of the same phyla or subclass in the rDNA based community) (1-(rRNA/rDNA)).

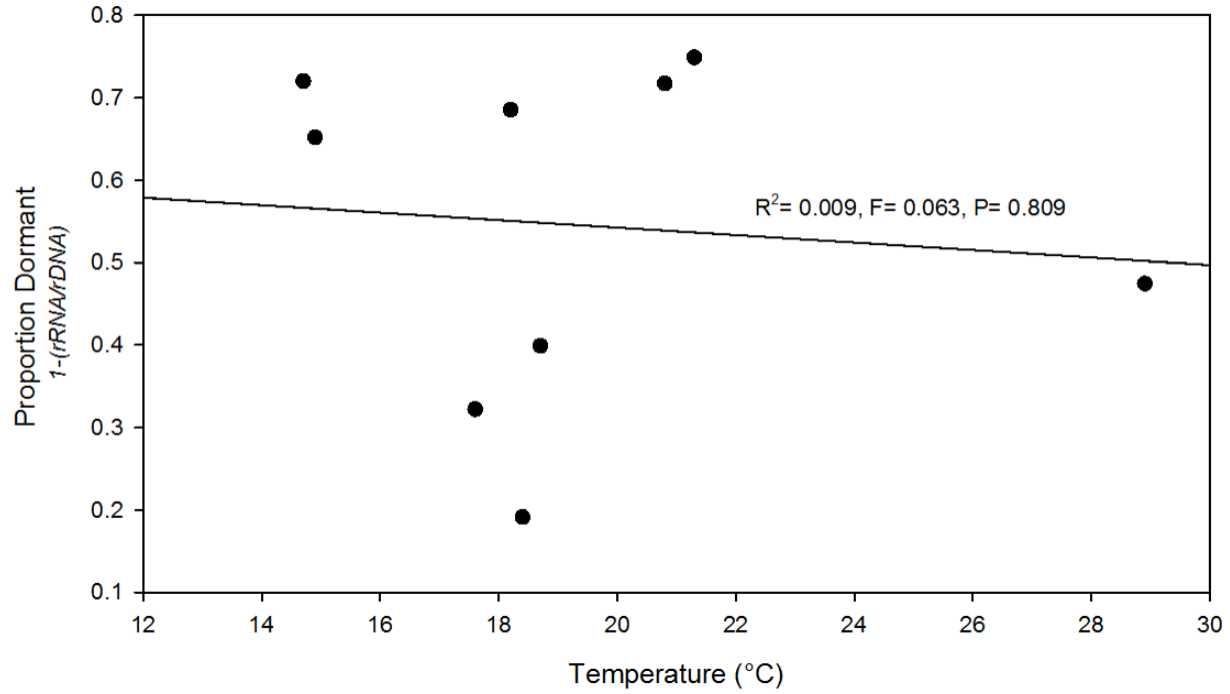


Figure S7. Linear regression of microbial dormancy for all lake samples plotted as function of temperature. Dormancy is calculated as 1-(relative recovery of a given phyla or subclass in the rRNA based community / relative recovery of the same phyla or subclass in the rDNA based community) (1-(rRNA/rDNA)).

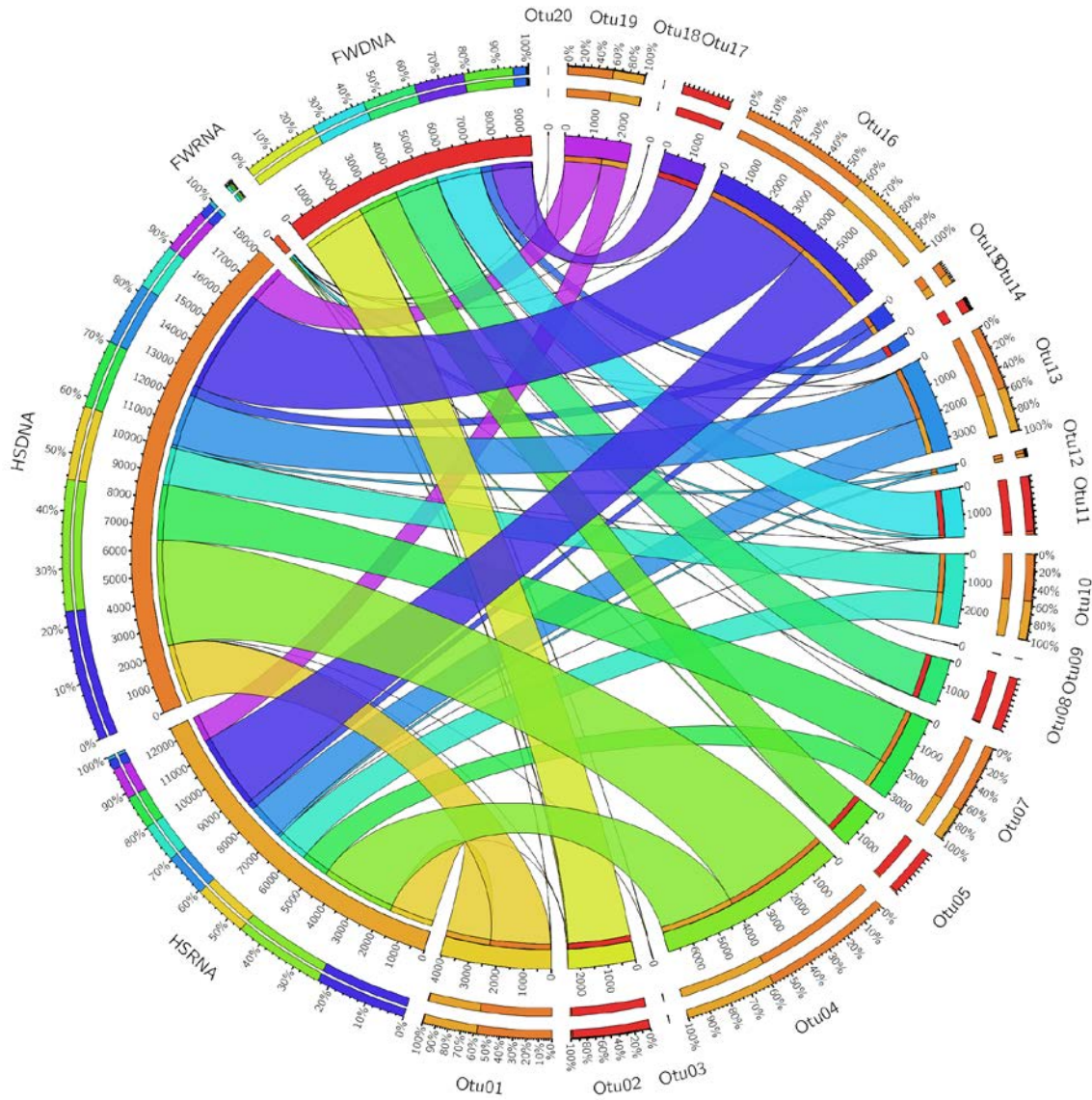


Figure S8. Circos graph generated to depict the DNA/RNA(cDNA)-based OTU redundancy for the first twenty OTUs in freshwater (FW) and hypersaline (HS) lake samples. Mothur open-source software distinguishes OTU1 is the most widely represented OTU across all samples; subsequent OTU output is numbered accordingly. Therefore, OTU 1-20 represent the most common species in all lake samples.

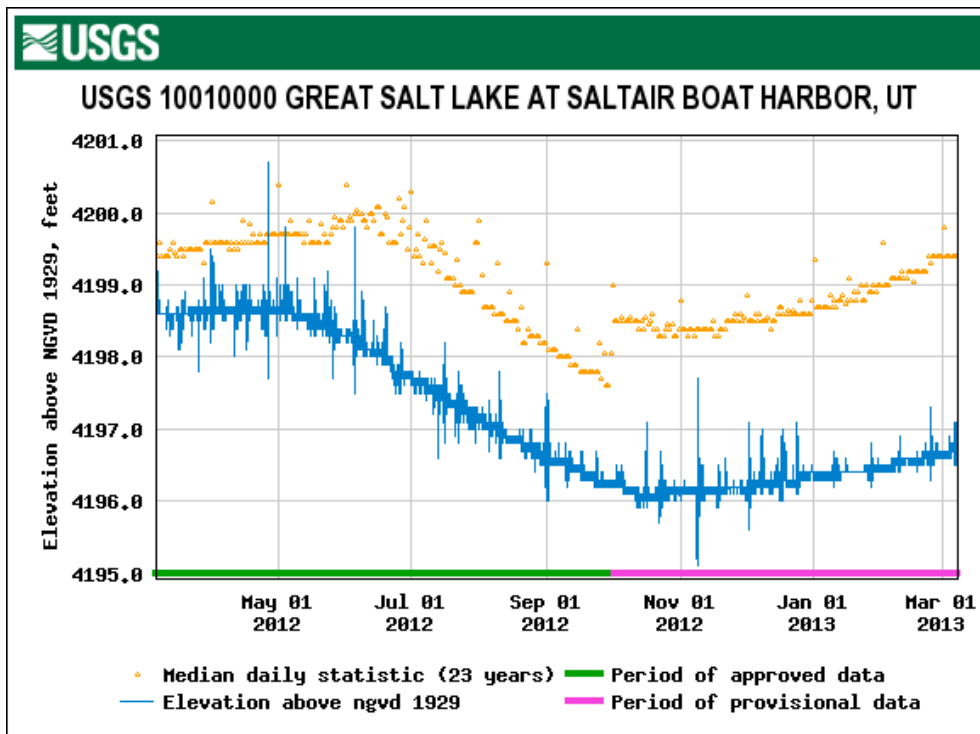
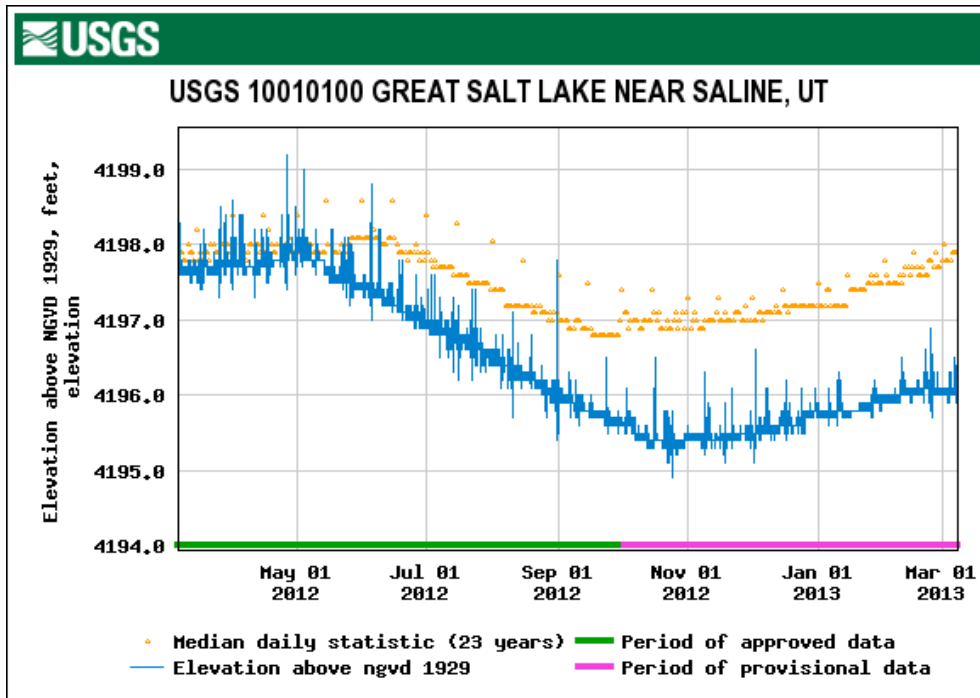


Figure S9. Great Salt Lake elevations measured at the Saltair Boat Harbor (southern arm) and Saline, UT (northern arm).