Factors affecting the spatial and temporal variability of cyanobacteria, metals, and biota in the Great Salt Lake, Utah

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February 10, 2015

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CHAPTER 1. FACTORS AFFECTING THE TOXIC CYANOBACTERIA *NODULARIA SPUMIGENA* IN FARMINGTON BAY OF GREAT SALT LAKE, UTAH

Eric McCulley and Wayne A. Wurtsbaugh

Summary

Farmington Bay is a 140 km^2 estuary that has restricted mixing with the saltier main body of the Great Salt Lake due to an automobile causeway on the north that connects the mainland and Antelope Island. The bay receives a significant amount of the nutrient-polluted discharge and runoff from Salt Lake and Davis Counties, Utah. This nutrient-laden runoff has led to anthropogenic eutrophication and seasonal blooms of the toxic cyanobacteria *Nodularia spumigena*. *Nodularia* has been observed in many brackish estuaries across the globe and contains the liver toxin nodularin. This study focused on understanding the physical and chemical factors controlling the growth of *Nodularia* in order to improve our knowledge about nutrients and the dynamics of phytoplankton in the Great Salt Lake.

In 2012 and 2013 sampling was conducted across the bay at nine locations during five separate sampling events to help understand the seasonal and year-to-year changes in *Nodularia*, where the salinity ranged from fresh water (2 g L^{-1}) to saline (80 g L^{-1}). The results showed that *Nodularia* densities and concentrations of the toxin nodularin exceeded World Health Organization "moderate" levels of adverse human health affect by as much as 1300%. The observed concentrations are also well above those that have caused water bird mortalities around the world. The maximum concentration of *Nodularia* was up to 1,358,000 cells mL^{-1} and nodularin reached 69 µg L^{-1}. However, *Nodularia* were not present at salinities >49 g L^{-1}. Correlation analysis and laboratory bioassays indicated that *Nodularia* responded to changes in both nutrients and salinity.

The relative concentrations of major nutrients changed along the gradient from the south to the north, with nitrogen increases possibly related to the fixation of atmospheric nitrogen by cyanobacteria.

Mean and maximum concentrations of total nitrogen were 5.2 and 7.8 mg L^{-1}, whereas those of total phosphorus were 0.57 and 3.5 mg L^{-1}. Mean and maximum chlorophyll *a* concentrations were 110 and 267 µg L^{-1}. Decreasing nutrient loading to the bay, or increasing salinities by making the automobile causeway more permeable, are possible management options to reduce *Nodularia* population in the bay.

Acknowledgments

We would like to thank Drs. David Stevens and Jennifer Follstad Shah, for their support and assistance in the design and writing of this chapter. Many people helped in the field and lab, provided comments on the direction of the research, or provided significant insights into the direction and interpretation of the research. These included: Audrey McCulley, Michael Stevens, Brian Barnes, Calah Seese, Susan Tahir, Erica Gaddis, Laura Vernon, Jodi Gardberg, Brian Nicholson, Marshall Baille, Leland Meyers, Theron Miller, Arthur Morris, Mark Morris, and Dave Barnes. Funding was provided by Utah Division of Forestry, Fire, and State Lands, the Utah Division of Water Quality and the Central Davis Improvement District.

Introduction

Background—Blooms of *Nodularia spumigena* (*Nodularia*) have been documented in Farmington Bay of the Great Salt Lake (GSL), USA over the last several decades (Hayes 1971, Felix and Rushforth 1978, Wurtsbaugh and Marcarelli 2005, Marcarelli et al. 2006, Wurtsbaugh and Epstein 2011, Wurtsbaugh et al. 2012, Marden et al. in prep.). Two key factors that affect the growth of algae and autotrophic cyanobacteria, such as *Nodularia*, include salinity and nutrient availability. Bioassays using water from the GSL, ranging in salinity from 10-160 g L^{-1} (1-16 %), have shown that *Nodularia* can grow in water with salinity of 70 g L^{-1}, but growth was strongest between 10-40 g L^{-1} (Marcarelli et al. 2006). The optimum salinity for *Nodularia* growth in experiments using water from the Baltic Sea and lakes in Australia was 5-20 g L^{-1} (Blackburn et al. 1996, Moissander et al. 2002). *Nodularia* have been shown to fix atmospheric N_2 at rates of 8-35 μmol C_2H_4 mg chlorophyll a^{-1} h^{-1} (Moisander et al. 2002, Marcarelli et al. 2006). Hence, *Nodularia* growth is often limited by phosphorus (P). Consistent with its N-fixing capacity, low total nitrogen (TN) to total phosphorous (TP) ratios have been correlated with higher production of *Nodularia* in the Gippsland Lakes, Australia (Cook and Holland 2012). Bioassays using water from the Farmington Bay showed that P additions stimulated *Nodularia* growth in long-term (30-day) studies (Marcarelli et al. 2006).

Previous studies have identified a physiochemical gradient that exists within Farmington Bay, where factors such as salinity and nutrients change in concentration from south to north (Marcarelli et al. 2006). Goel and Meyers (2009) found little or no *Nodularia* in open water areas in the far southern extent of Farmington Bay where salinities were low. More recent studies (Marden et al. in prep.) have shown more widespread *Nodularia*, still mostly found in the middle and north part of the bay. Other studies have also found increasing concentrations of *Nodularia* and cyanotoxins along the south to north gradient (Marcarelli et al. 2006, Wurtsbaugh and Epstein 2011). Previous studies have also documented pronounced seasonality in *Nodularia* blooms, which peak from May-July, but can still persist into the fall.

Our study helps to shed additional light on how salinity and nutrient limitation regulate the growth of *Nodularia* in Farmington Bay. We found *Nodularia* concentrations above 100,000 cells mL^{-1}, and nodularin concentrations well above 20 µg L^{-1}, which are the World Health Organization's moderate risk level for contact with human skin (Chorus and Bartram 1999). Also, water collected for previous bioassay experiments was not collected during the early spring into summer, which may have affected the interpretation of results on nutrient limitation. Consequently, we conducted two experiments to determine if nutrient limitation changes along the gradient from south to north. In another bioassay experiment we modified salinity to determine its role in regulating the growth of cyanobacteria and other phytoplankton. We also collected zooplankton to assess whether their grazing pressure might be sufficient to decrease phytoplankton abundance. The observations presented here help us further understand how nutrients and biota interact, within the existing physical landscape and across time, so we can better understand the spatial and temporal variation of the algal blooms.

Watershed Context—Farmington Bay is located at the downstream end of the Jordan River watershed and receives surface runoff and secondary-treated waste water from the Jordan River, several small streams, state-run waterfowl management areas and wetland outfalls, the Salt Lake Sewage Canal, and waste water treatment plants in northern Salt Lake County and Davis County. In all, a total of thirteen waste water treatment plants serving approximately 1.5 million people provide inputs of water and nutrients to the bay. Some of this water has been filtered through managed wetlands and private duck clubs, but much of the water entering the bay is secondary-treated waste water.

The total watershed area of Farmington Bay is approximately 9,000 km^2 (3,500 square miles), which is the most highly-urbanized land in Utah. The bay covers approximately 140 km^2 (50 square miles), with depths at our sampling stations ranging from 0.2 meters (8 inches) to 1.5 meters (60 inches). The flow in Farmington Bay is from south to north (Figure 1). Mixing of Farmington Bay with the main lake (Gilbert Bay) is restricted by Antelope Island on the west, and an automobile causeway on the north.

Bi-directional exchange of water between Farmington Bay and the more saline Gilbert Bay is primarily through a 16.5 meter (50 foot) breach/bridge near the west end of the causeway (Figure 1).

Farmington Bay is recognized as internationally important for migratory birds, has a beneficial use class of 5D, which has the designated use to protect for infrequent primary and secondary contact recreation, waterfowl, shorebirds, and other water- oriented wildlife including their necessary food chain. Farmington Bay includes Antelope Island and south of the Antelope Island Causeway (UDWQ 2012).

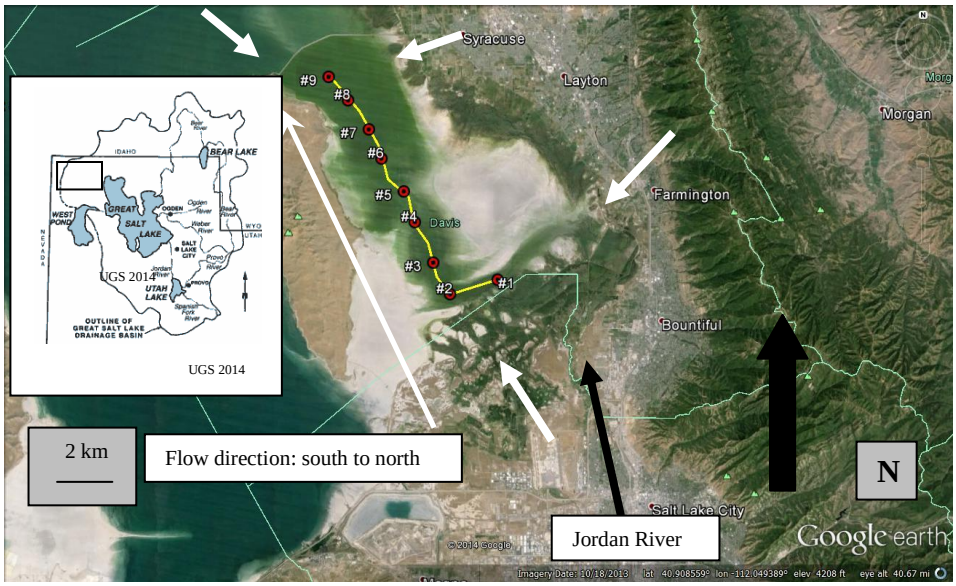

Figure 1. Overview of Farmington Bay showing some inputs. The arrow spanning the bay indicates the direction of flow in the bay from south to north. The smaller white arrows to the northeast, east and south indicate urban or wastewater treatment plant inflows, white arrow to the north shows the causeway, and the small black arrow indicating the location of the Jordan River. The circles show the sampling stations used in the transect.

Whereas many communities around the world are concerned about *Nodularia* and other toxin producing cyanobacteria due to drinking water concerns, Farmington Bay is not used for drinking water, thus the issues are different. There have been reports of foul odors, bird deaths due to avian disease, and high levels of the liver toxin nodularin, but no significant environmental or human health impacts of these *Nodularia* blooms in Farmington Bay have been documented. It was important for us to study the bay in order to determine if *Nodularia* blooms are common and if they have any adverse effect on the beneficial uses.

Methods

Five separate sampling events were conducted at nine locations (Figure 1) along the physical and chemical gradient in Farmington Bay during the spring and autumn of 2012 and the spring and summer of 2013. These sampling points were selected to cover the length of the bay and were evenly spaced with approximately 1.6 km (1 mile) between each location. The Utah Division of Water Quality collects samples at two stations in the north end of the bay as part of the GSL Comprehensive Water Quality Strategy (UDWQ 2012). The location of those sampling points corresponds with our sampling Stations 7 and 9.

Study Site and Field Sampling

Field sampling was conducted at each location along the transect in June and September of 2012; and in May, early June, and late June of 2013. These sampling periods were selected because they represent distinct periods during the spring, summer, and autumn seasons where relative concentrations of nutrients and salinity were expected to be distinctly different, and when blooms of cyanobacteria have previously been highest (Wurtsbaugh et al. 2012). Particulate material (seston) in the water from Central Davis Sewer District outfall, two locations on the lower Jordan River (above and below the South Davis Sewer Improvement District outfall), and one sample from the Salt Lake Sewage Canal at Cudahey Lane (lat. 40.8424° / long. -111.9500°) was also collected on June 20, 2012 and analyzed for comparison with isotopic signatures found across the bay. This was done to determine: (1) if wastewater from the treatment plants might influence the isotopic signature, and (2) if varying levels of nitrogen fixation along the south to north gradient lowers the $\delta^{15}N$ signal or if there were any interesting trends in carbon isotopes

At each site vertical profiles of temperature, oxygen, and conductivity were completed at 0.2 meters increments using an InSitu® data sonde. Salinity was measured with a refractometer and changed to units of g L^{-1} using the following equation derived from hundreds of measurements in the Great Salt Lake (Wally Gwynn, unpublished):

$$\text{Salinity (g L}^{-1}) = 0.08164\ (\%\ \text{Salinity})\ 2 + 9.96334\ (\%\ \text{Salinity}) - 0.43533 \quad (1)$$

Water for nutrient analyses, phytoplankton, cyanotoxins, pigments, and isotope samples were collected at "elbow-depth" or approximately 0.2 meters below the surface for laboratory analysis. Light attenuation was measured with a 20-cm diameter Secchi disk. Zooplankton were collected using a vertical haul of a 0.3 meter diameter, 153-µm meshed zooplankton net. However, on the first sample date half of the samples were collected in 2.0 liter jugs. The 153-µm mesh size should have collected nearly all the crustacean zooplankton, but most rotifers would have passed through it. During the May and late-June transects in 2013, water samples were collected at every other station for analysis of total mercury (Hg), methylmercury (MeHg), arsenic (As), copper (Cu), lead (Pb), cadmium (Cd), selenium (Se), and thallium (Tl). Additionally, Hg and Se in zooplankton samples were analyzed from these stations, but these parameters are discussed in a separate report. Table 1 provides a detailed list of laboratory samples and field parameters collected during each transect.

Table 1. Matrix of laboratory analyses and field parameters done in 2012-2013 in Farmington Bay.

No. Stations per transect		2012		2013		
	Lab samples	**JUN 18-19**	**SEP 21**	**MAY 03**	**JUN 03**	**JUN 28**
9	Total and dissolved nutrients	¤	¤	¤	¤	¤
9	Chlorophyll *a*	¤	¤	¤	¤	¤
9	Phycocyanin	¤	¤	¤	¤	¤
9	$\delta^{13}C$ and $\delta^{15}N$ Isotopes	¤		¤	¤	¤
5	Algal taxonomy	¤		¤	¤	¤
5	Cyanotoxins (nodularin)	¤		¤	¤	¤
5	Zooplankton abundance	¤	¤	¤	¤	¤
1 or 3	Bioassays	3			3	1
	Field parameters					
9	Temperature and salinity	¤	¤	¤	¤	¤
9	Total depth, Secchi depth	¤	¤	¤	¤	¤

Analytical Methods—All water samples were first processed in the Limnology Laboratory at USU for chlorophyll *a*, phycocyanin, and zooplankton. Other parameters were analyzed at various commercial laboratories, as indicated in Table 2. To measure chlorophyll *a*, 10 mL of water was filtered through 1-µm Gelman A/E filters and frozen. Chlorophyll *a* from the frozen filters was extracted in 10 ml of 95% ethanol for 20-24 hours and analyzed with the non-acidification method of Welschmeyer (1994) on a Turner 10-AU fluorometer. A pigment indicative of cyanobacteria, phycocyanin, was analyzed with a Turner 10AU filter kit which provided relative concentrations measured in Turner fluorometer units (TFU).

Nutrient samples from 0.2 meters were collected in 2.0 liter polyethylene bottles in the field and were analyzed for nitrate + nitrite ($NO_3 + NO_2$), ammonium (NH_4), total nitrogen (TN), soluble reactive phosphorus (including phosphate [PO_4]), and total phosphorus (TP). Raw water for total nutrient concentration was frozen at -20 C, and subsequently analyzed as described below. Water for dissolved nutrients was filtered in the laboratory using vacuum filtration pressures < 33 x 10^3 Pa through 1-μ m Gelman A/E filters and stored in polyethylene bottles at -20 C until analyzed using the persulfate digestion method of Valderrama (1981) using an Astoria Pacific autoanalyzer.

To measure $\delta^{15}N$ and $\delta^{13}C$ of particulate material in the water column, samples were filtered using a pre-weighed and pre-combusted, 25-mm Gelman AE filter. Samples for isotopic analysis were sent to the University of California - Davis Isotope Facility for analysis using GC-combustion isotope ratio mass spectrometry.

Algal composition in glutaraldehyde-preserved water sampled from the transects was determined by an outside laboratory (Phycotech, St. Joseph, MI). Identification and biovolume estimates were completed by mounting samples in resin on slides and counting and measuring cells at 100x-1000x magnification to the level of genus or species, where possible.

Concentrations of the toxin nodularin were analyzed with EnviroLogix (Portland, Maine) enzyme-linked immunosorbent assays (ELISA; Quantiplate Kit for detection of microcystin) by Limnology Lab personnel utilizing facilities in the Center for Integrated Biosystems at USU. Not all samples fell within the range of detection for the ELISA standards. Nodularin levels were derived by using a 0.73 correction factor on the microcystin measurement following EnviroLogix protocol (EnviroLogix 2010).

The composition of zooplankton at every other sample location (Stations 1, 3, 5, 7, and 9) was analyzed using a dissecting microscope at 15-30x power after collection in the field. The total sample was

shaken to allow for even distribution of organisms and a subsample was taken with a Hensen-Stempel pipette and put into a zooplankton counting chamber. All organisms in the subsample were identified to species using a higher magnification (up to 100x) then 10 individuals of each taxa were counted and measured using a micrometer scale at 30x. Measurements were used to calculate biomass following the length-weight regressions shown below given in McCauley (1984) and listed in Table 2, where α is equal to the length of the organism in millimeters (mm) and dry weight is in micrograms (µg):

$$\text{Weight} = \alpha * (\text{Length})^{-\beta} \qquad (2)$$

Table 2. Zooplankton length to weight coefficients used to derive the zooplankton biomasses from Reeve (1963) and McCauley (1984).

Taxa	Organism size (mm)	α	β
Artemia	4.9 (avg.)	0.9	3.0
Copepods	0.14-2.45	7.0	2.4
Daphnia	0.6-4.00	4.3	2.8

Bioassays—Three laboratory bioassays were conducted to test the influence of nutrients and salinity on chlorophyll *a*, phycocyanin, and nodularin levels. For each experiment, bottles were incubated in a light- (150 µMol cm^{-2} sec^{-1}) and temperature- (20°C) controlled environment and agitated twice daily.

The June 4, 2013 bioassay was conducted with nutrient additions that were approximately 3x ambient background levels. In order to develop a better understanding of how nutrient limitation might vary across the spatial extent of the bay, naturally varying levels of salinity in lake water from three stations were used (see Table 3). Experiments were conducted with water collected from stations 1, 5 and 9 which provided phytoplankton communities growing at salinities ranging from 3-37 g L^{-1}. Nutrients were added to 900 mL glass jars with plastic tops. Each salinity combination was replicated three times

for each treatment with control, +N, +P, and +N+P additions of 35 mg N (as NH_4NO_3) L^{-1} and 0.5 mg P (as Na_2HPO_4-$7H_2O$) L^{-1}. Chlorophyll *a*, nodularin and phycocyanin (as a measure of cyanobacterial levels) levels were analyzed before the bioassay commenced (as part of initial field sampling) and on day eight.

Two additional experiments were conducted between June 29 and July 5, 2013 using water collected on June 28, 2013. These experiments included an additional nutrient limitation bioassay and a salinity alteration experiment, both using water from Station 5. The initial salinity of water from this station was 16 g L^{-1}. For the salinity alteration experiment, salinity was increased using 400 mL of the raw lake water mixed with 400 mL of saline solution, which was created by mixing InstantOcean® aquarium salt to provide salinity treatments ranging from 16-59 g L^{-1}. To insure that phytoplankton in these treatments were not nutrient limited, N and P were also added to all of the jars at the same concentration used in the N+P bottles in the nutrient addition bioassay on June 28.

Table 3. Design of the three bioassays using water collected from different stations in Farmington Bay on June 3 and 28, 2013. In the Salinity Assay, salt concentrations were increased with InstantOcean® aquarium salt above the background concentration of 16 g L^{-1} measured at Station 5. The ¤ symbol indicates nutrients that were added to bottles in each experiment.

Nutrient Addition Bioassay (June 3, 2013)					
Station	**Salinity**	**N**	**P**	**N and P**	**control**
Station 1	**3 g L^{-1}**	¤	¤	¤	¤
Station 5	**16 g L^{-1}**	¤	¤	¤	¤
Station 9	**37 g L^{-1}**	¤	¤	¤	¤
Salinity Bioassay (June 28, 2013)					
Station 5	**16 g L^{-1}**			¤	¤
Station 5	**26 g L^{-1}**			¤	
Station 5	**37 g L^{-1}**			¤	
Station 5	**48 g L^{-1}**			¤	
Station 5	**59 g L^{-1}**			¤	
Nutrient Addition Bioassay (June 28, 2013)					
Station 5	**16 g L^{-1}**	¤	¤	¤	¤

Statistical Methods—Field data were analyzed using Pearson's product-moment correlation or linear regression using R (R Core Team 2014) to determine if there were any correlations between physical and chemical parameters as compared to cyanotoxins, *Nodularia*, phytoplankton levels, and pigment concentrations. Results of the bioassay experiments were analyzed in R using a one-way analysis of variance (ANOVA), with log-normalized values to meet ANOVA assumptions. Post-hoc Tukey's Studentized Range tests were used to evaluate which treatment responses were significantly different from each other.

Results

The results of the study are discussed below first by physical parameters, which outline the south to north environmental gradient that is typically present in the bay. Chemical parameters such as nutrients and isotopes are then discussed, followed by phytoplankton and related parameters such as phycocyanin, chlorophyll *a*, the hepatotoxin nodularin and zooplankton densities. The final section provides observations of the laboratory bioassays, which help us understand both nutrient limitation and salinity controls on phytoplankton.

Environmental Conditions - gradients in physical factors

During the study, the depth of our sampling stations ranged from 0.2 meters at the south end to over 1.5 meter at the north end. The water in the bay generally flowed in a northerly direction and spanned about 3 kilometers (1.9 miles) across, or one-third of the total width when the bay is at a higher elevation. Temperature ranged from 13-29°C, which is within the range tolerated by *Nodularia* in other parts of the world (Hobson and Fallowfield 2003, Mazur-Marzek et al. 2006). Secchi depths ranged between 0.14 m to 1.1 m (Figure 2). The depth at which photosynthesis can occur is approximately 2-3x Secchi depths. Consequently, sufficient light for photosynthesis was usually available throughout most of the shallow water column at most locations.

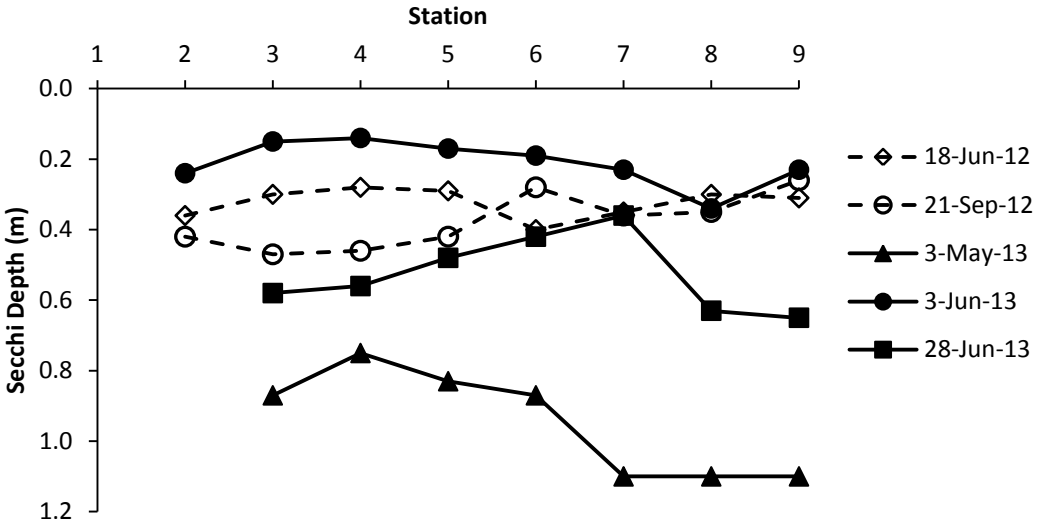

Figure 2. Secchi depth at the nine transect locations on five dates in 2012 and 2013. The water clarity at Station 1 was always greater than the maximum depth (0.2-0.5 m) so Secchi depth measurements were not possible at that location. On two transects Secchi depths were also greater than the maximum depth (0.4-0.6 m) at Station 2.

Chemical Gradients

Salinity

Spatial and temporal variation in the salinity was high across the bay during the study (Figure 3). During the runoff period in May and June of 2013, salinities ranged from 1-4 g L^{-1} near the freshwater inflows in the south, to 26-37 g L^{-1} in the north. In 2012, a low runoff year, salinities were higher, both in June, and particularly in September when they reached 74 g L^{-1} at the north end of the bay.

Nutrients

Total nitrogen concentrations were generally high in the bay, ranging from a low of 1.6 mg L^{-1} to over 7 mg L^{-1} (Figure 4). The nutrient concentrations differed across the bay on each of the different dates, but there were some similarities in patterns (Figure 4). Nitrogen patterns were similar on different

dates, but the peak of TN shifted between sample events. For example, TN peaked at over 7 mg L^{-1} at Station 3 on June 3, 2013 and peaked at a similar level at Station 6 on September 21, 2012. TN was high across the bay on May 3, 2013 (3-4 mg L^{-1}) and increased approximately 2-fold by June 28, 2013 to over 7 mg L^{-1}. Dissolved inorganic nitrogen (ammonia, nitrate, and/or nitrite) had different patterns across the dates with a NH_4^+ maximum of 1.2 mg L^{-1} and NO_3^- maximum of 1.1 mg L^{-1} at Station 9 on September 21, 2012. On June 3, 2013 there was a consistent increase in dissolved inorganic nitrogen from the south to the north in the bay.

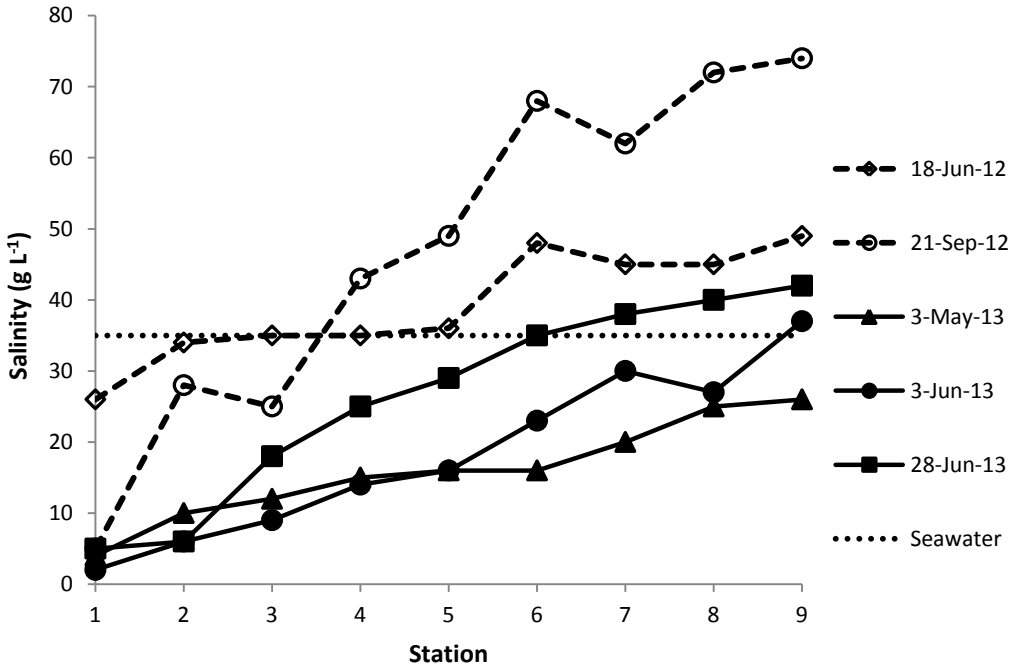

Figure 3. Salinities at the nine transect stations in Farmington Bay on five dates in 2012 and 2013. The salinity across the bay changes from south (Station 1) to north (Station 9) and is also variable based on the time of sampling. Seawater is represented at a dashed line at 35 g L^{-1} salinity. As shown, the salinity in the bay changes from below that of seawater to above, creating a complex interaction with physical parameters, nutrients and biota. Note that the salinities at most stations during the second year were below that of seawater.

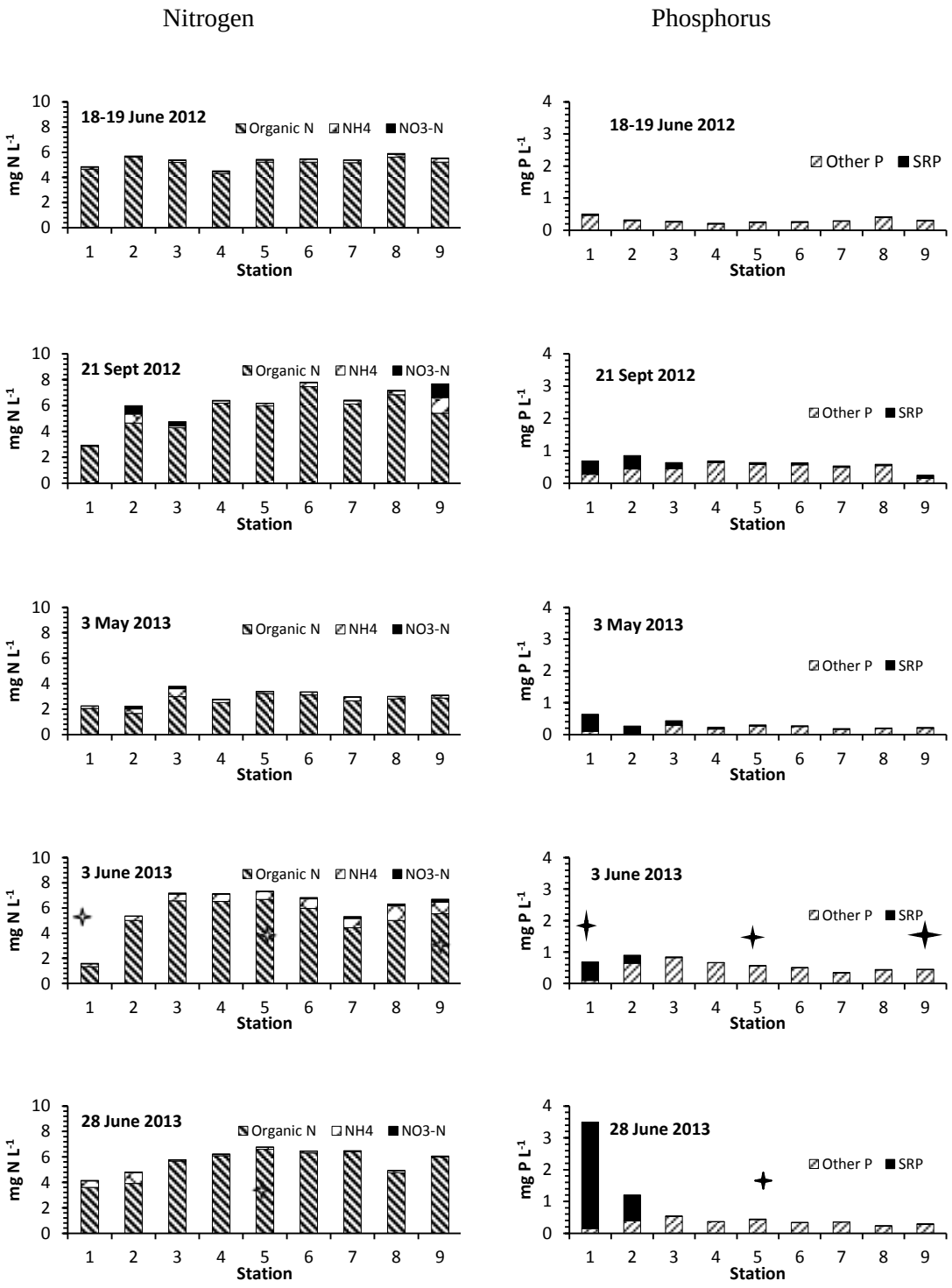

Figure 4. Nutrient concentrations in the surface (0.2 m) water at nine stations in Farmington Bay for the five transects completed in 2012-2013. The top line on these charts represents the total nitrogen (TN) and total phosphorus (TP) in the samples. ✧ Denotes stations where bioassay water was collected. SRP = soluble reactive phosphorus.

Total phosphorus concentrations were fairly consistent across the bay, but with slightly higher concentrations in the south end (Figure 4). Soluble reactive phosphorus (SRP) was most pronounced in the south end of the bay and was consistently reduced to very low or non-detectable concentrations (below 0.01 mg L^{-1}) by Station 3.

TN:TP ratios always increased from the southern-most stations to the north (Figure 5). At Stations 1 and 2 the TN:TP ratio was usually below or near the Redfield ratio of 7.2:1 (by mass), but further north the ratio increased to more than 15:1. The increase in this ratio indicates increasing P limitation as you go to the north. If the Redfield ratio is applicable in the bay, the nutrient limitation may change from N limited in the south to P limited in the north end of the bay.

Isotopes—The results of the isotope ratios for $\delta^{15}N$ and $\delta^{13}C$ in the bay and from some specific sources showed consistent trends across the bay, with minor variations for each date (Figures 6 and 7). Sources included the Jordan River above and below the South Davis Improvement District South Outfall, the Salt Lake Sewage Canal, and the Central Davis Improvement District. The water collected from the Central Davis Improvement District outfall showed the highest level of $\delta^{15}N$ (+15.6), which is typical of sewage effluent (Onodera et al. 2015). The reduction in $\delta^{15}N$ from the source areas in the south (left) to the north (right) indicate increasing levels of atmospheric nitrogen (with $\delta^{15}N$ of 0.0) may have been fixed by cyanobacteria. The Salt Lake Sewage Canal and the Central Davis Improvement District outfall showed the highest values in comparison to levels across the bay, which decreased (became more negative) to the north.

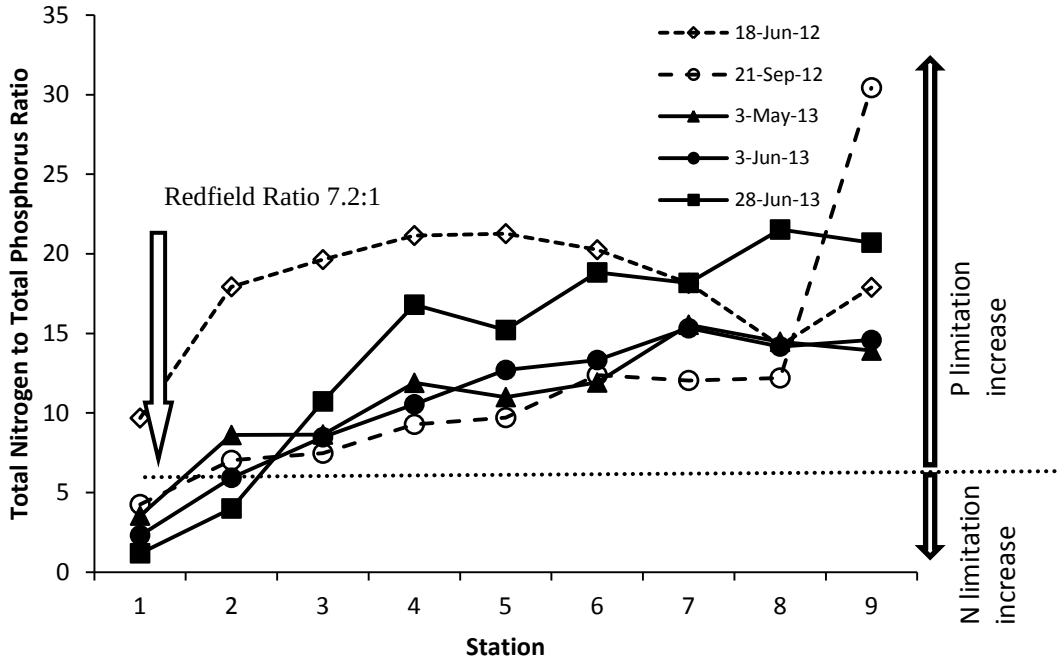

Figure 5. Total nitrogen to total phosphorus ratios across the bay on each transect date. The general trend of TN:TP is to increase from south to north, with the exception of June 18, 2012. This trend indicates increasing P limitation towards the north. The N:P ratios giver here are based on weight:weight.

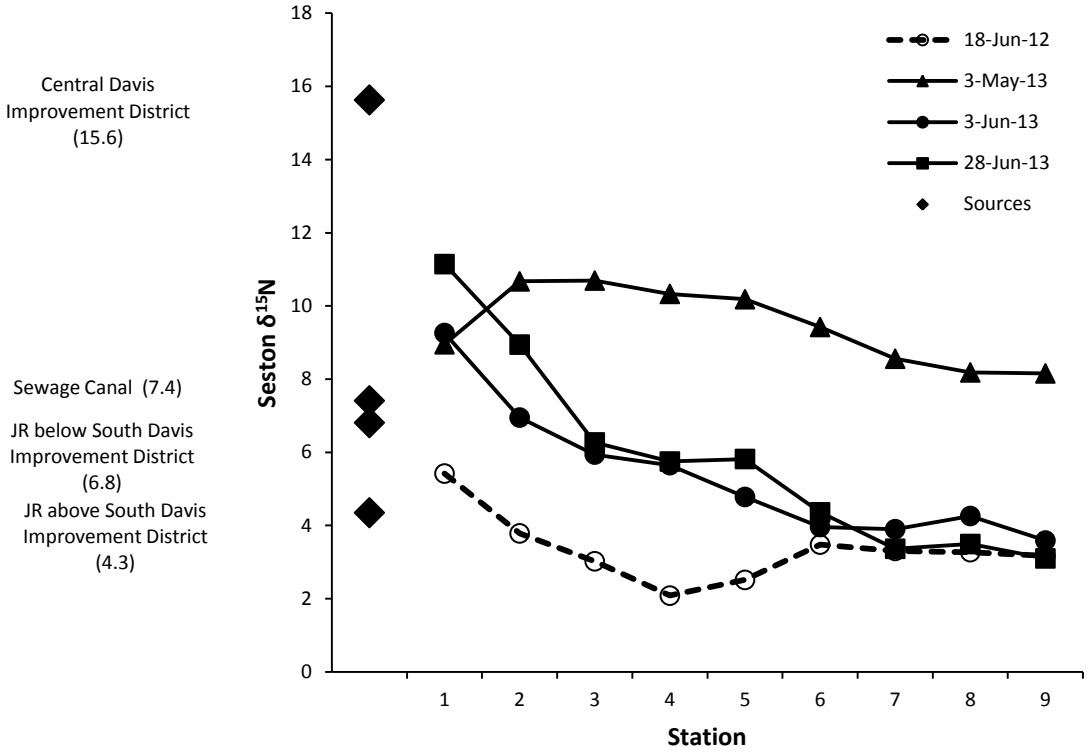

Figure 6. Particulate material $\delta^{15}N$ levels at nine stations across Farmington Bay on four dates. $\delta^{15}N$ levels of four wastewater discharges (♦) and the Jordan River (JR) that enter at the south end of the bay are plotted to the left of the Station 1 data and were collected on June 20, 2012.

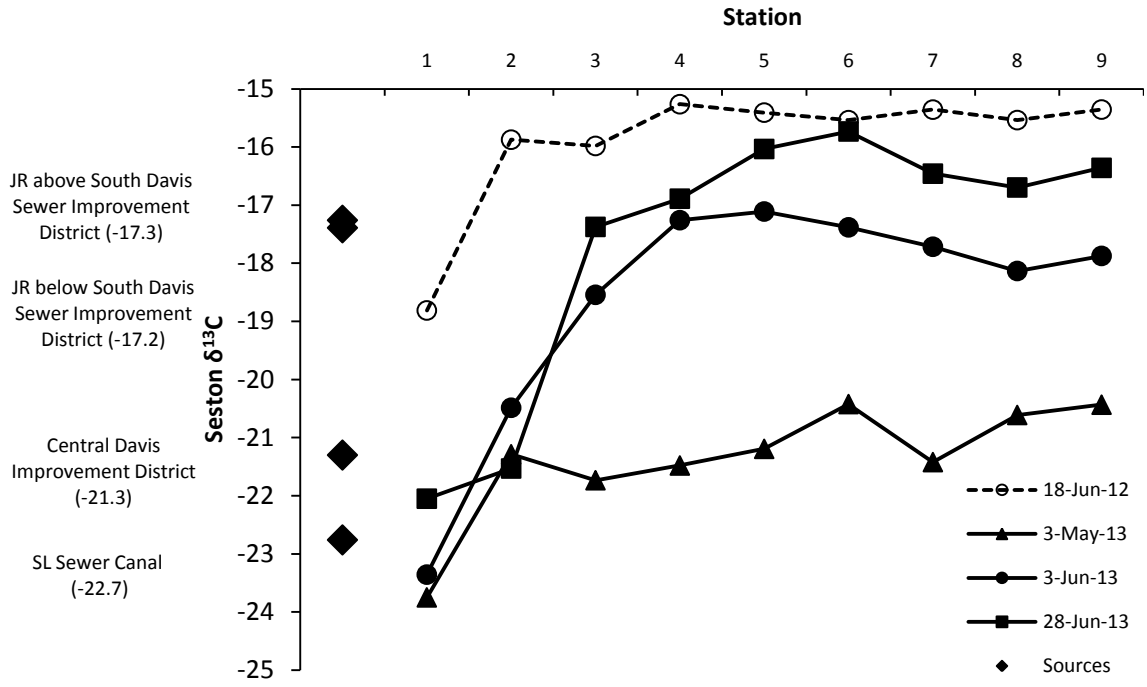

Figure 7. Particulate material $\delta^{13}C$ across Farmington Bay with some source water levels on the left of the chart. $\delta^{13}C$ levels of four wastewater discharges (♦) and the Jordan River (JR) that enter at the south end of the bay are plotted to the left of the Station 1 data and were collected on June 20, 2012.

The $\delta^{13}C$ values also changed across the bay, generally increasing from south to north (Figure 7). Particulate matter in the Salt Lake Sewage Canal and Central Davis Sewer District outfall showed the most negative values for $\delta^{13}C$ and most values across the bay were similar to those found in the Lower Jordan River.

Cyanobacteria and other phytoplankton

On most dates and at most stations, cyanobacteria dominated algal cell density in Farmington Bay (Figure 8). Other abundant taxa included Bacillariophyta (diatoms) and Chlorophyta (green algae), which had different abundances and distribution depending on the time of the year. In general, the highest levels of both cyanobacteria and phytoplankton were observed in June for both years, but the temporal extent of

our study was limited. On some dates Bacillariophytes and Chlorophytes had a larger percentage of the total concentrations in the bay. The difference between concentrations on each of these dates indicates that there can be major swings in the biota on any given period.

On June 18, 2012 the highest levels of cyanobacteria (primarily *Nodularia*) were observed at Station 3, which is approximately 3 km (2 miles) north of the outfall for the Salt Lake Sewer Canal, with up to 1.3 million cells mL^{-1} (Figure 8). This level was approximately 1500% of the World Health Organization's (WHO) indicator level for "moderate" effects with exposure to human skin, which is 0.10 million cells mL^{-1}. Diatoms and green algae were relatively consistent across the bay representing 10-30% of the cell count.

The June 3, 2013 sampling date showed a similar pattern with the cyanobacteria peak at Station 3, but concentrations were slightly lower than June, 2012, but still were 700% of the WHO "moderate" health risks of exposure to skin for humans. Green algae also peaked at Station 3 with concentrations of 15-20% of the total phytoplankton, with a similar peak in diatoms at >10% of the total.

On September 21, 2012, the cyanobacteria species shifted away from the *Nodularia* domination to that of *Synechocystis* sp. at the south end and *Pseudoanabaena* sp. at the north (Appendix C). *Pseudoanabaena* can produce the hepatotoxin microcystin (Paerl and Otten 2012), which is similar to the nodularin produced by *Nodularia*. *Synechocystis* can also produce cyanotoxins. Green algae were also a larger component of the cell concentration towards the north end of the bay.

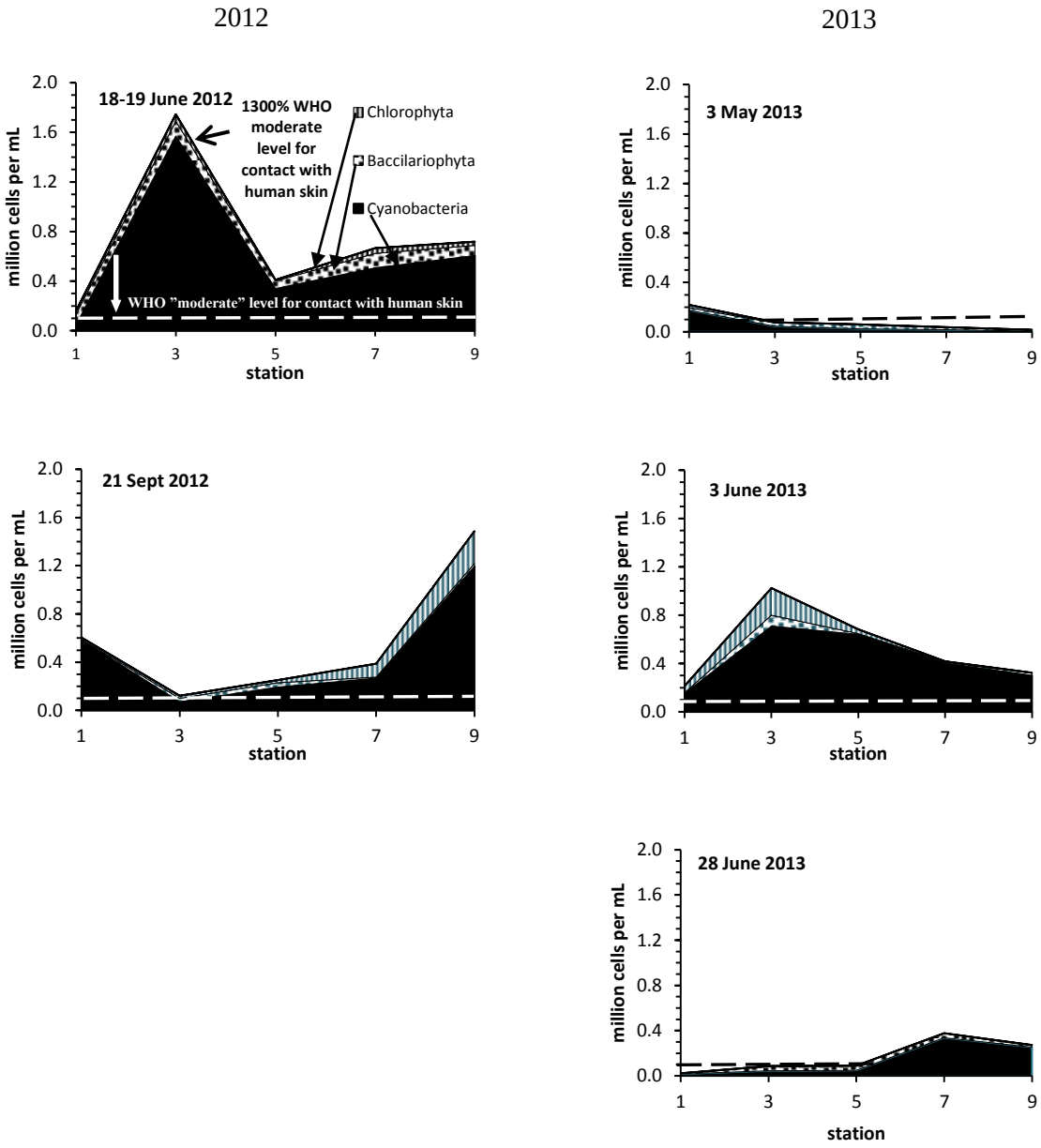

Figure 8. Cyanobacteria (blue-green algae), bacillariophyta (diatoms) and chlorophyta (green algae) concentrations in on five dates at Stations 1, 3, 5, 7, and 9 along the transect in Farmington Bay. Cyanobacteria (primarily *Nodularia*) dominated and the dashed line at 0.1 million cells mL^{-1} of cyanobacteria indicates where the World Health Organization (WHO) has designated a "moderate health risk" for human exposure to skin. Other taxa were usually insignificant in number.

The cyanobacteria and phytoplankton densities on May 3 and June 28, 2013 were relatively low compared to the other dates. In May there were more cyanobacteria (*Synechocystis*) at the south end than at the north end and in late June there were more cyanobacteria (*Nodularia*) at the north end.

Densities of *Nodularia* were highest on June 18, 2012 and were present in most of the phytoplankton samples we collected (Figure 9). In both years of this study, the highest *Nodularia* concentrations were found in June, but the limited number of sample dates did not cover the entire year, so higher values may have occurred on other dates. *Nodularia* concentrations were lower on the three other dates and a few samples were at or below the WHO risk level for moderate health effects from contact.

The cyanotoxin nodularin was observed at most locations on all dates, with the exception of September 21, 2012, when *Pseudoanabaena* was the most prevalent cyanobacteria. The highest levels of nodularin were observed on June 3, 2013 at 69 µg L^{-1} (LR equivalent microcystin), which is well above moderate risk of human contact limits of 20 µg L^{-1} of microcystin (Figure 10).

Chlorophyll *a* levels averaged 110 µg L^{-1} across all samples in the study with a maximum of 263 µg L^{-1} at Station 3 on June 3, 2013 and a minimum of 1.3 µg L^{-1} at the south end of the bay on September 21, 2012 (Figure 11). Total phytoplankton biovolume measured at the different stations and dates was weakly but significantly correlated with chlorophyll *a* levels (Pearson's $r = 0.56$, $t = 3.52$, $df = 27$, p-value $= 0.0015$).

Total nitrogen concentrations were weakly correlated to concentrations of *Nodularia* (Figure 12). The correlation with TN was partially driven by the low concentration of *Nodularia* on May 3, 2013. TP was not correlated with *Nodularia* (Figure 13).

Phycocyanin levels, a metric of cyanobacterial abundances, were significantly ($p < 0.001$) log-linearly correlated with nodularin concentrations (Figure 14). This analysis did not include all of the

stations where nodularin may have been present because levels sometimes fell outside of the range of ELISA standards. This result indicates that phycocyanin may be a good indicator for nodularin when *Nodularia* is the most prominent cyanobacteria.

Nodularia biovolume was limited to salinities below 48 g L^{-1} and phycocyanin was also mostly limited by salinity to below 48 g L^{-1}, with the exception of values recorded from water collected on September 21, 2012 when *Pseudoanabaena* sp. was present at salinities as high as 78 g L^{-1} (Figures 15a and 15b).

Zooplankton densities and biomass estimates

The density and biomass of zooplankton were highly varied between dates and were also extremely high on some dates (Figure 16). The most common zooplankton in the bay included *Moina macrocarpa*, other cladocera, harpacticoid copepods, and calanoid copepods, with smaller numbers of *Artemia fransicana*, corixids, and *Daphnia* spp. On June 18-19, 2012, *Moina* were the most abundant organism observed with some *Artemia fransicana* also observed. On September 21, 2012, corixids had increased to become the dominant organism across the bay in terms of biomass. In 2013, *Moina* were the most abundant organism for both densities and biomass, but densities and biomass of both copepods was also significant. On May 3, 2013, concentrations and biomasses of *Moina* and copepods were consistent across the bay, with an increase in Artemia at the north end of the bay. On June 3, 2013, density and biomass of *Moina* and the copepods was highest in the central portion of the bay with increased concentrations of harpacticoid copepods and *Artemia* was also present in the north end of the bay. On June 28, 2013, *Daphnia* spp. was present in the south end of the bay, but was not observed north of the southern-most point along the transect. On the later date, copepods also increased in the middle of the bay, but *Moina* dominated by the north end of the bay and no *Artemia* were observed.

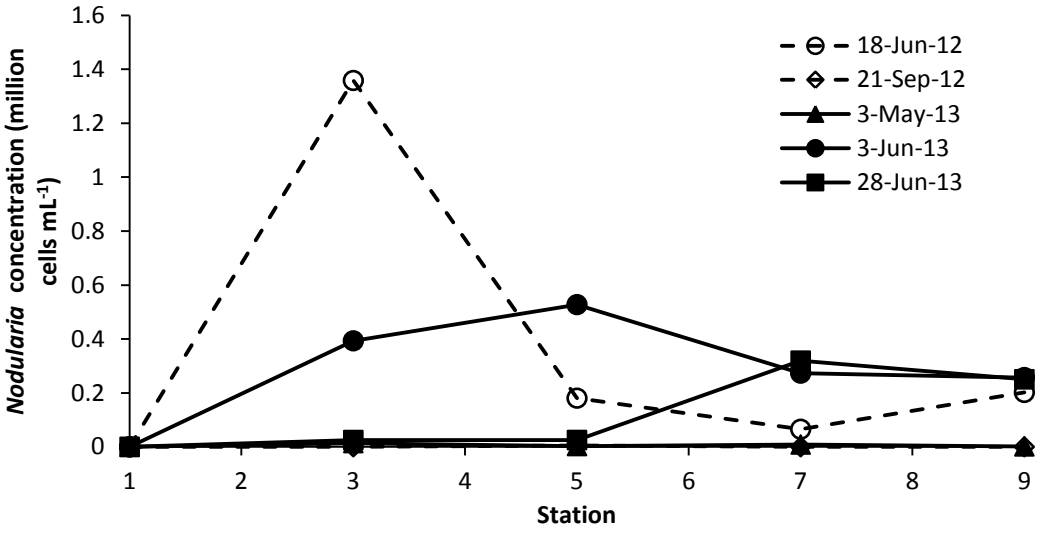

Figure 9. Concentrations of *Nodularia spumigena* at five stations on five dates in Farmington Bay. Concentrations on 21 September 2012 were all near zero and the data points are hidden by other symbols.

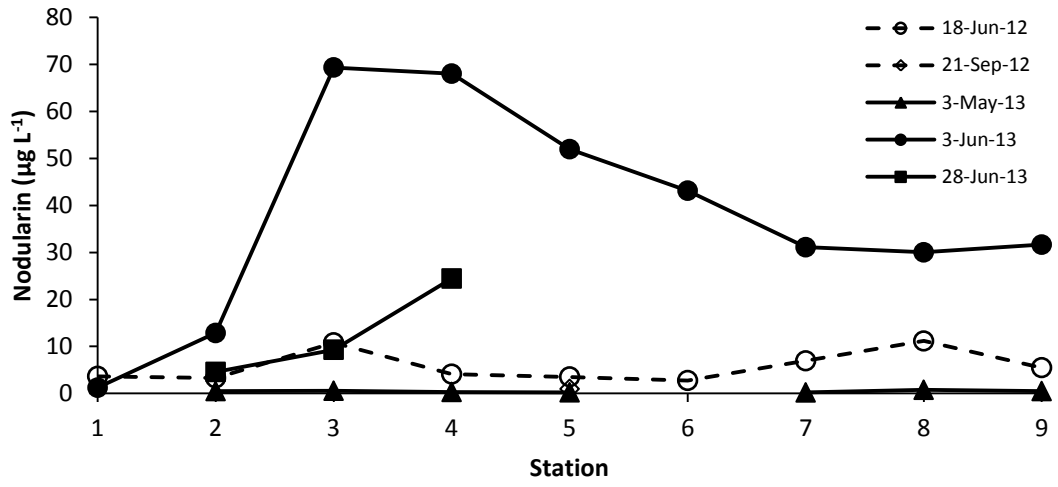

Figure 10. Cyanotoxin nodularin concentration across Farmington Bay on five dates. The level of nodularin, which is a liver toxin (hepatotoxin) was far above World Health Organization levels for "moderate" health effects on humans with exposure to skin (20 µg L^{-1}) on June 3, 2013. On some dates and stations, nodularin concentrations were outside of the range used in our standards.

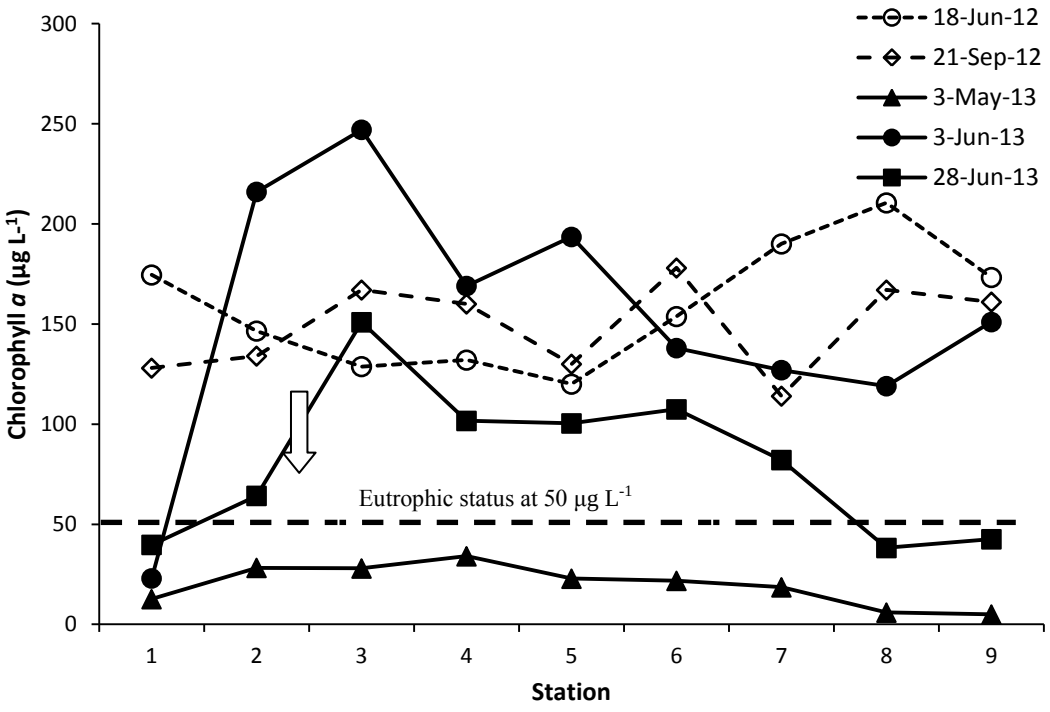

Figure 11. Chlorophyll *a* levels across Farmington Bay on five dates in 2012 and 2013. The horizontal dotted line at 50 µg L^{-1} shows the criteria for eutrophic classification using fresh water criteria (Carlson 1977).

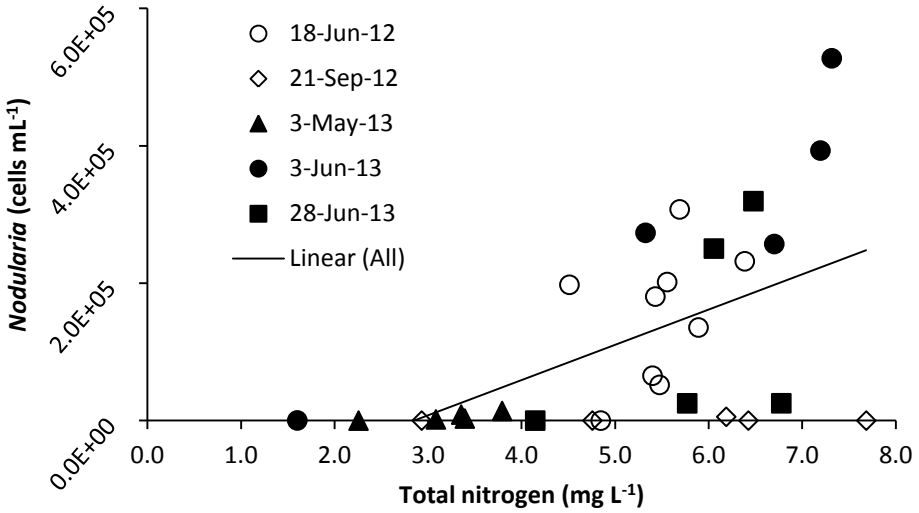

Figure12. Relationship between total nitrogen and *Nodularia* cell density measured at five transect stations on five dates in 2012 and 2013. Total nitrogen to *Nodularia* concentration in cells per mL showed a weak but significant correlation (Pearson's r = 0.55, t = 3.425, df = 27, p-value = 0.0020).

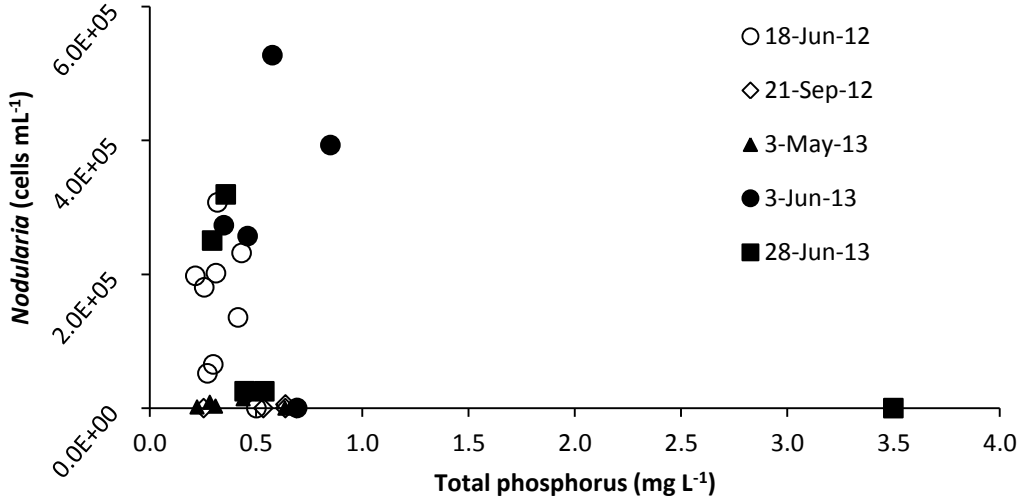

Figure 13. Relationship between total phosphorus and *Nodularia* cell density measured at five transect stations on five dates in 2012 and 2013. These two variables were not significantly correlated (p = 0.79).

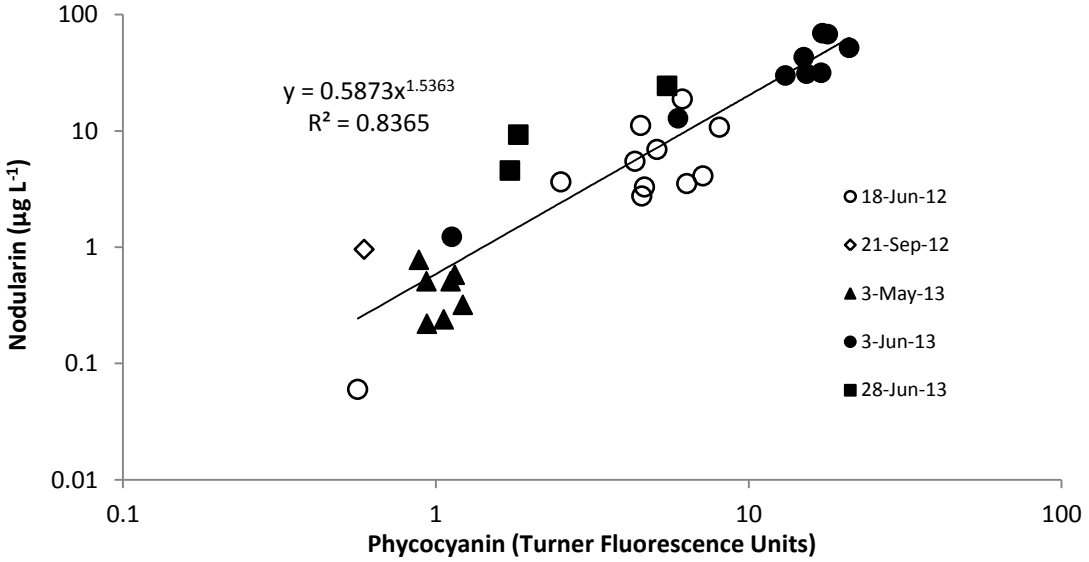

Figure 14. Correlation between concentrations of the cyanobacterial pigment phycocyanin and nodularin toxin measured with ELISA ($p = 0.00001$). Note the large ranges in phycocyanin pigment and nodularin depicted in this log-log plot.

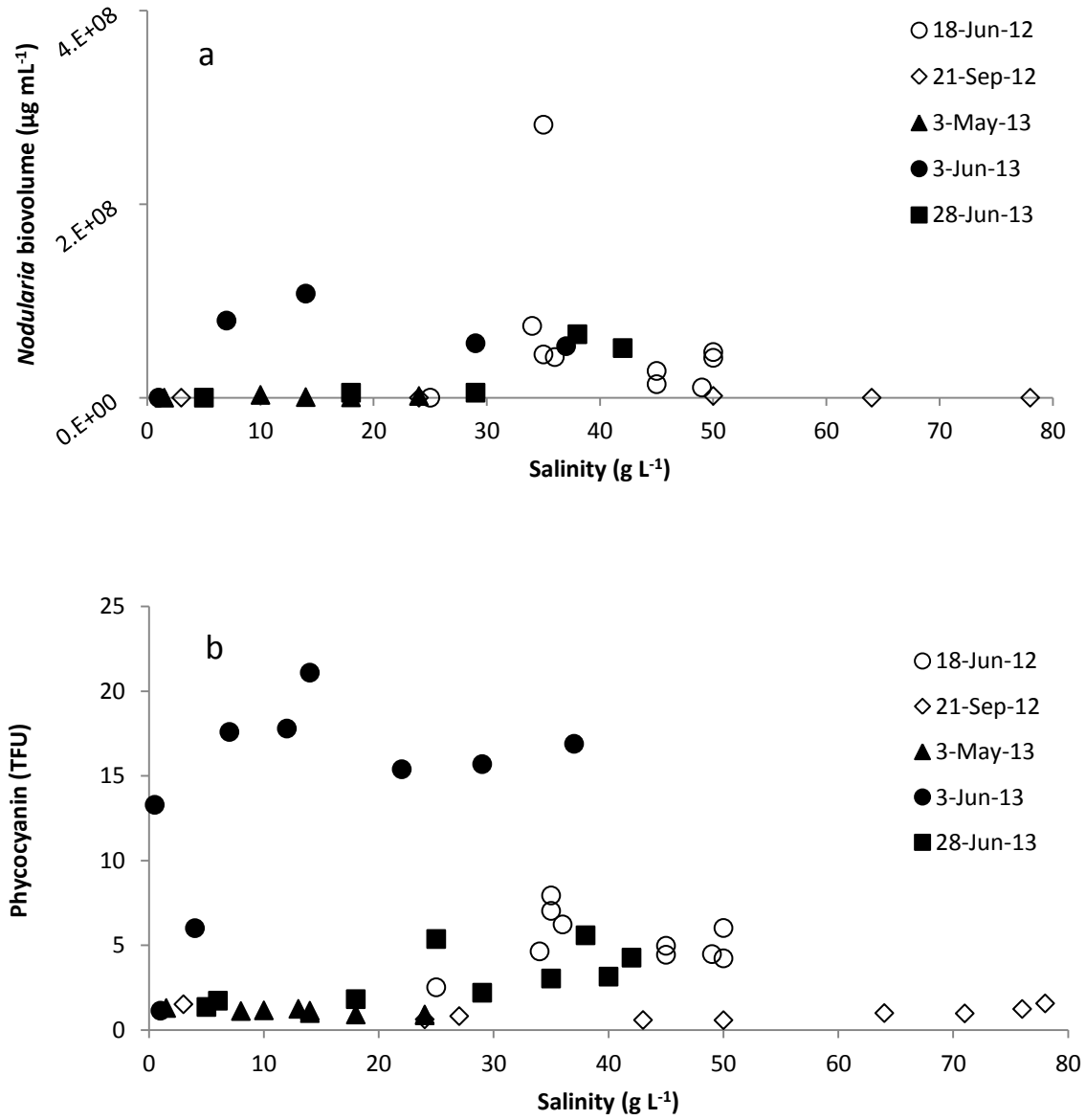

Figure 15. a) *Nodularia* biovolume as a function of salinity along transects in Farmington Bay in 2012 and 2013. Note that *Nodularia* was not found above 48 g L^{-1} salinity. b) Concentrations of phycocyanin pigment, a proxy for cyanobacterial biomass, along the transects. The low levels of phycocyanin pigment observed on September 21, 2012 at salinities above 50 g L^{-1} were from *Pseudoanabena* sp. (see Appendix C).

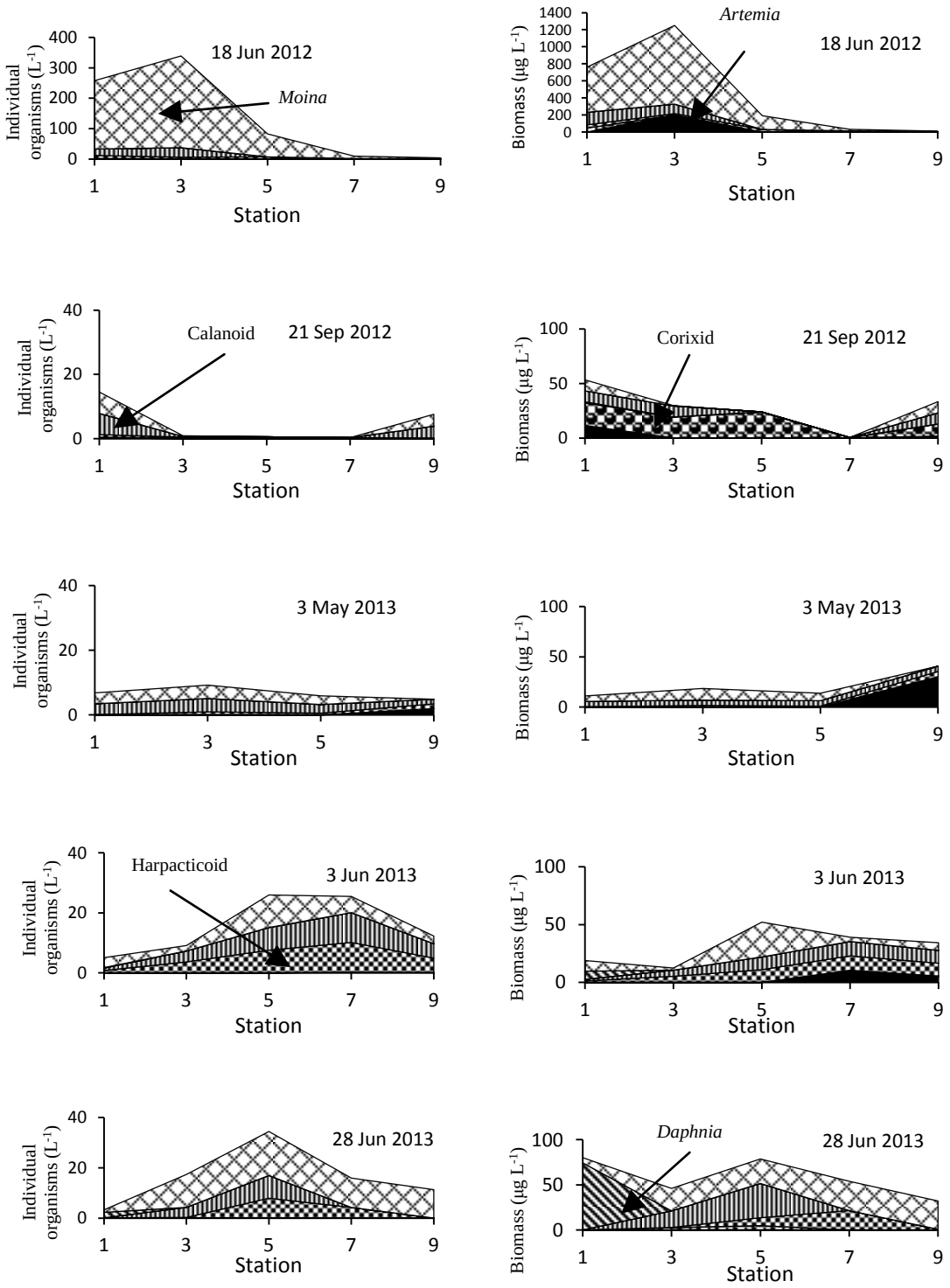

Figure 16. Zooplankton densities (left) and biomasses (right) at five stations along the Farmington Bay transects. Note different scales used on June 18, 2012 when abundances were extremely high.

Bioassay results

June 3, 2013 Nutrient addition bioassay—The results indicated that nitrogen was the primary limiting nutrient, but there were different responses across the bay (Figure 17). Water from Station 1 at the south end of the bay the initial biovolume of taxa was dominated by diatoms (35%) and chlorophytes (46%), with only 7% cyanobacteria (Appendix C), and overall densities were moderate (Figure 8). At this station N and +N+P stimulated the production of chlorophyll *a*, but phosphorus alone did not stimulate the phytoplankton. There was also a stimulation of the cyanobacterial pigment phycocyanin with the addition of N and concentrations in the +N+P treatment were not significantly higher than in the +N treatment, indicating that P had no influence on pigment production. Similarly, addition of P alone did not result in any significant change in pigment concentrations. These results indicate that phytoplankton and cyanobacterial growth the south end of the bay was likely nitrogen limited on June 3, 2013.

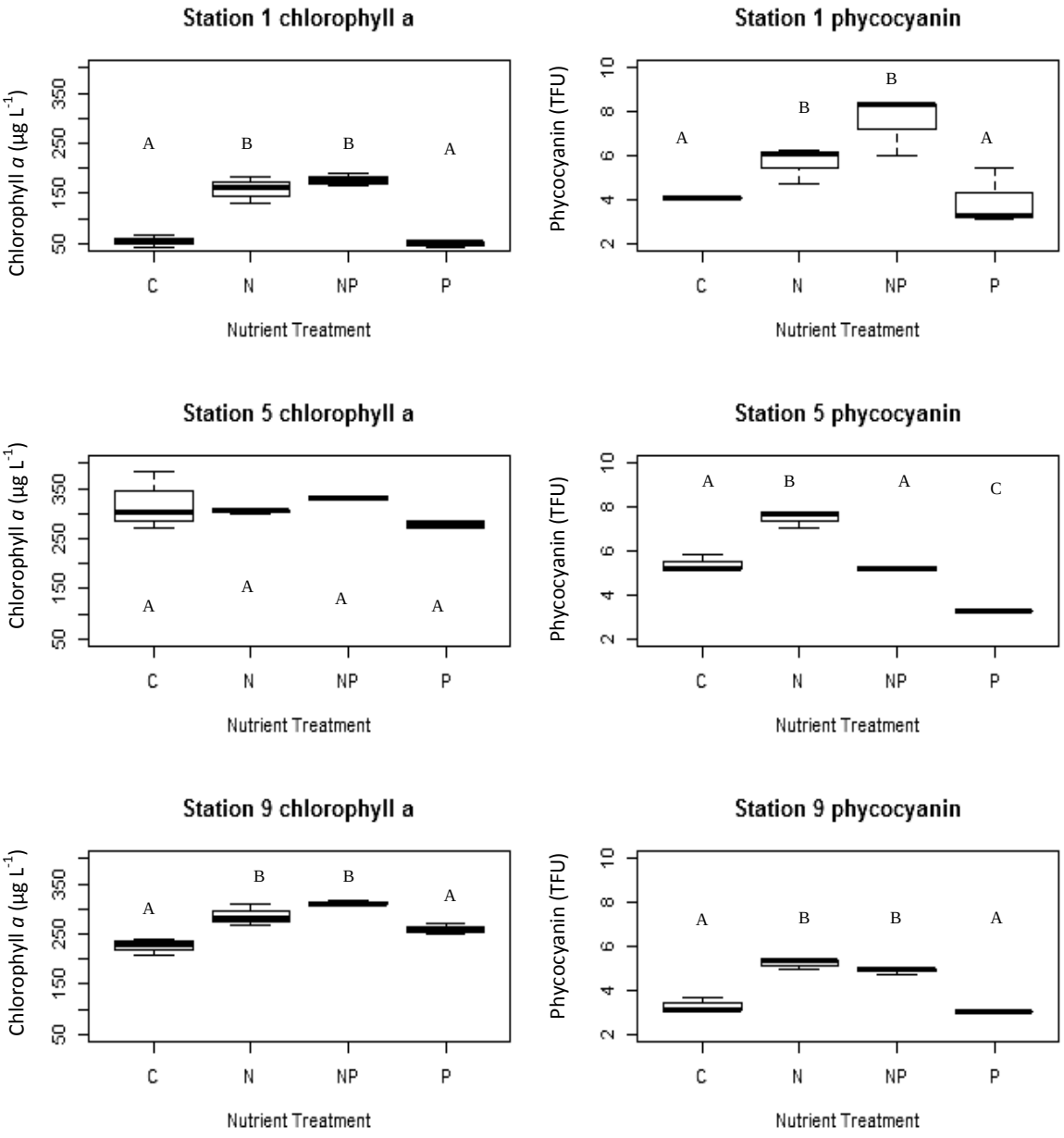

Figure 17. Boxplots of chlorophyll *a* (µg L^{-1}) and phycocyanin (Turner fluorescence units [TFU]) at the end of an 8-day nutrient addition bioassay experiment using water from three locations along the transect from south to north from water collected on June 3, 2013. Means are represented as thick black lines and ranges are represented with the whiskers. Treatments in the experiment were: C-Controls; N-NH_4NO_3 additions; P-PO_4 additions, and; NP-additions of both NH_4NO_3 and PO_4. Stations 1, 5, and 9 were located at the southern, middle, and northern parts of the bay, respectively. One-way analyses of variance done for each station indicated that there were significant differences between treatments, with the exception of Station 5 chlorophyll *a*. Letters indicate significant differences between specific treatments as determined by post-hoc Tukey's Studentized range tests. Treatments that share a common letter were not significantly different.

The initial phytoplankton biovolume at Station 5 was high and composed of 96% *Nodularia* (Appendix C). At this station in the middle of the bay chlorophyll *a* did not respond significantly from additions of N or P. Phycocyanin was increased with the addition of N and significantly reduced by the addition of P, but strangely a combination of both did not result in any significant difference. These results indicate that the cyanobacteria growth (as measured by phycocyanin) in the middle of the bay may have been limited by N, but other phytoplankton growth (as measured by chlorophyll *a*) was not limited by nutrients and instead may have been limited by another factor such as light or zooplankton grazing, which was high at this location. At Station 9 (the north end of the bay) the addition of N and +N+P stimulated both phycocyanin and chlorophyll *a*, but P additions did not increase either parameter. These results indicate that both phytoplankton and cyanobacteria growth was N-limited at that location.

June 28, 2013 nutrient addition and salinity bioassays—Water collected at station #5 in the middle of the bay was used to conduct two bioassay experiments designed to: 1) determine if any nutrient limitations existed at this location, and 2) determine if there was an effect from varying the salinity on the growth of cyanobacteria and phytoplankton, as measured by phycocyanin and chlorophyll *a*. The initial phytoplankton composition of the cultures was dominated by diatoms (64%, primarily *Cyclotella* sp.), and *Nodularia* (32%), but overall cell densities were low (Figure 8).

Nutrient addition bioassay—Both phycocyanin and chlorophyll *a* increased in controls from the starting value, but only phycocyanin levels showed a significant difference from the control at the end of the experiment ($p=0.0005$; Figure 18, lower frames). Phycocyanin concentrations increased with the addition of both N+P, but not when either nutrient was added separately. Chlorophyll *a* did not show a significant response to N, P or N+P, but the concentration did increase over 200% compared to the starting value measured on the day of field collection.

Salinity treatment bioassay – Both phycocyanin and chlorophyll *a* showed significant differences from the control (salinity not altered and remained at 17 g L^{-1}), but these measures responded in opposite

B

A

directions to the changes in salinity (Figure 18, upper frames). Phycocyanin levels decreased as salinities increased from 17 g L^{-1} to 43 g L^{-1}, but did not significantly change above that level. In contrast, chlorophyll *a* levels increased significantly with each salinity increment from 17 g L^{-1} through 58 g L^{-1}.

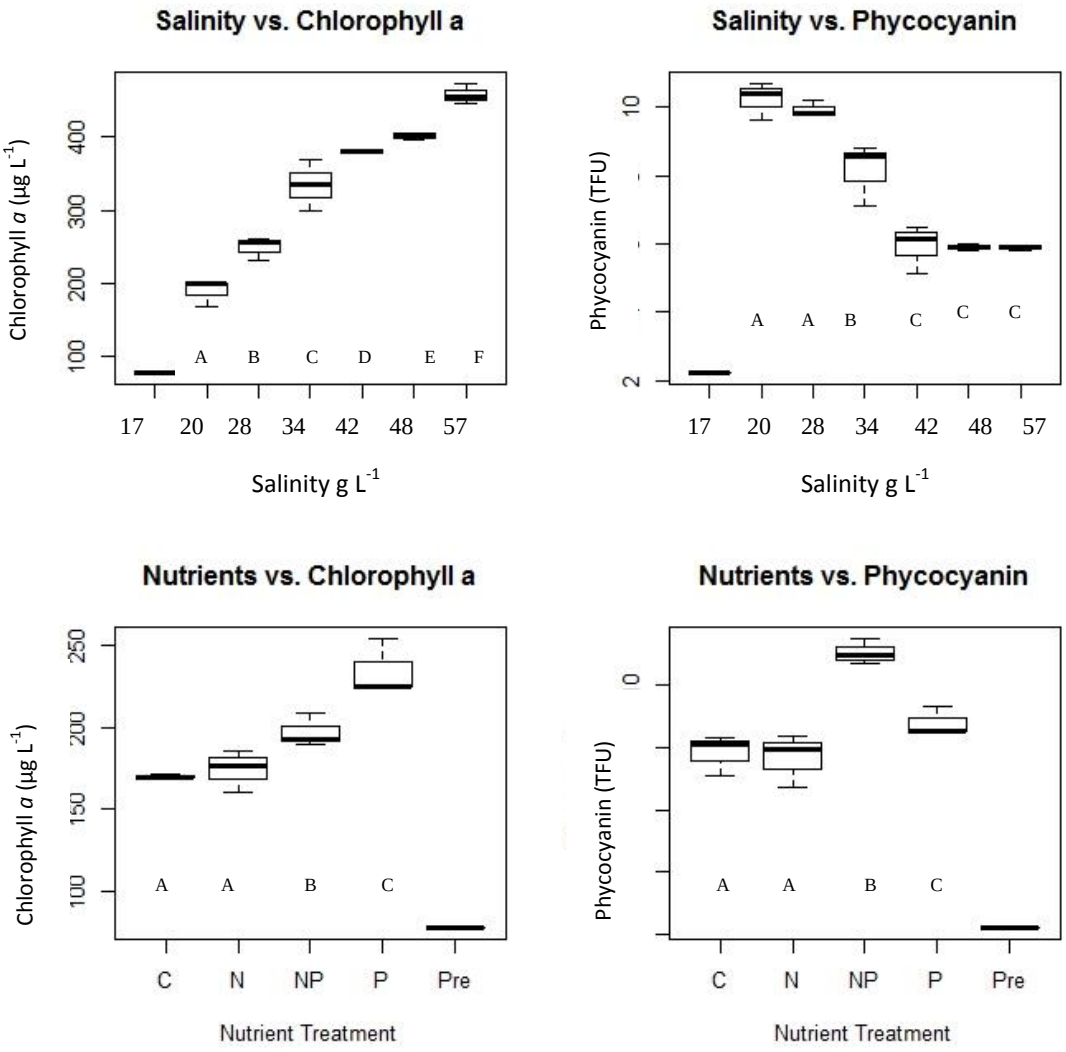

Figure 18. Chlorophyll *a* and phycocyanin concentrations in nutrient addition and salinity change bioassays conducted over 8 days starting on June 29, 2013. These bioassays used water from the middle of Farmington Bay (Station 5). The values for the 18g L^{-1} salinity indicate the phycocyanin or chlorophyll levels in the lake water at the start of the experiment. Bars indicate max, min and mean (dark bar) and boxes indicate quartiles. One-way analysis of variance indicated that there were significant differences between treatments and control for some treatments but not all. Letters indicate significant differences as determined by post-hoc Tukey's Studentized range tests. Treatments that share a common letter were not significantly different.

Discussion

Nodularia, cyanotoxins, and eutrophication

The results of our study confirm that *Nodularia spumigena* is commonly found in Farmington Bay and the levels of it, and the toxin it produces, often exceed the World Health Organization's (WHO) advisory levels for adverse aquatic human health effects. We collected data on the concentration of *Nodularia* at five locations across the bay on five different dates and found that concentrations often exceeded 100,000 cells mL^{-1}, which is the WHO's moderate risk level for contact with human skin (Chorus and Bartram 1999). These values are comparable to concentrations found in other studies of the bay (Wurtsbaugh and Marcarelli 2005, Wurtsbaugh 2007, Wurtsbaugh et al. 2012, Marden in prep.; Table 4). We found a mean concentration of nodularin of 14 µg L^{-1} and a maximum level of 69 µg L^{-1} on June 3, 2013. Concentrations were often above the 20 µg L^{-1} level identified as moderate human health risk by the WHO (Chorus and Bartram 1999). These conditions can be toxic to aquatic organisms, birds, and mammals (Francis 1878, Paerl and Otten 2012, Drobac et al. 2013) and may have adverse impacts on nearby human populations if the cyanobacteria cells or cyanotoxins become entrained in dust storms blowing over populated areas (Metcalf et al. 2012).

Table 4. *Nodularia* concentration ranges (cells mL^{-1}) found in four studies of Farmington Bay.

This study	Marden et al. (in prep.)	Wurtsbaugh et al. (2012)	Wurtsbaugh and Marcarelli (2005)
0 - 1,358,000	0 - 900,000	0 – 1,640,000	0 - 897,000

Accounts of ecological and human health disasters related to cyanotoxins are common across the globe and there is little doubt that human inputs of nutrients usually cause the high concentrations that precipitate such events (Paerl and Otten 2012, Drobac et al. 2013). Other studies across the globe have also found direct or indirect links between blooms of *Nodularia* and toxic effects on mammals, including

humans (Francis 1878, Nehring 1993, Mazur-Marzec et al. 2007, Simola et al. 2012, Drobac et al. 2013). Nonetheless, the official status of Farmington Bay is that the water meets the beneficial uses in the bay, including the needs of wildlife and aquatic life and the recreation needs of humans. Additionally, Farmington Bay is not typically used for contact recreation. Furthermore, there is no definitive information to link the cyanobacteria blooms and cyanotoxins to ill effects on wildlife or aquatic life in the Great Salt Lake. Many instances of harm to birds and aquatic organisms, possibly related to cyanobacteria exposure, have been recorded in recent years around the globe (e.g. Matsunaga et al. 1999, Alonso-Andicoberry et al. 2002, Landsberg 2002, Blaha et al. 2009, Da Ferrao-Filho and Kozlowski-Suzuki 2011, Paerl and Otten 2012, Lurling and Faasen 2013). Many of these events have occured at cyanobacteria densities and toxin levels well below those that have been observed in Farmington Bay.

The results of our study also confirm that hypereutrophic conditions occur regularly in the bay, where we observed mean and maximum chlorophyll *a* concentrations of 110 µg L^{-1} and 263 µg L^{-1}, respectively, across all samples in the study (Table 5). These concentrations are well above the 50 µg L^{-1} designating a hypereutrophic classification (Carlson 1977) and are comparable to those observed in previous and ongoing studies (Wurtsbaugh and Marcarelli 2005, Wurtsbaugh 2012, Marden et al. in prep.). These hypereutrophic conditions have led to periods of anoxia throughout the water column, which may not be suitable to support aquatic life at all times (Wurtsbaugh 2012). Although there were highly variable conditions across the bay during our study, some general patterns were observed. Similar to the patterns seen in many inland lakes (Lampert et al. 1986), we saw diatom and green algae growth early in the year to mid-June, transitioning into mostly cyanobacteria in mid-summer of 2013. Although densities of mostly herbivorous zooplankton such as *Moina* sp. and *Daphnia* sp. were frequently very high (Figure 16), their grazing pressure was apparently unable to keep up with the growth of cyanobacteria and other phytoplankton.

Table 5. Mean and peak chlorophyll *a* concentrations (µg L^{-1}) found in four studies of Farmington Bay.

	This study	Marden et al. in prep.	Wurtsbaugh et al. 2012
Mean	110	NA	141
Peak	263	506	470

Salinity Gradient as an Ecosystem Driver

The spatial extent and variability of cyanobacteria and other phytoplankton across the bay was related to salinity. We observed *Nodularia spumigena* in water with salinity between 7 and 50 g L^{-1}. Marden et al. (in prep) reported that no *Nodularia* was present over 59 g L^{-1} salinity in a concurrent study. This threshold for the persistence and growth of *Nodularia spumigena* is higher than that found in the Baltic Sea, where *Nodularia* is typically found between 7 to 20 g L^{-1} salinity. Lehtimaki et al. (1997) and Moissander et al. (2002) found that growth of *Nodularia* from the Baltic was inhibited above and below those thresholds. The results of our bioassays conducted between June 29, 2013 and July 5, 2013 showed that the pigment phycocyanin decreased and chlorophyll *a* increased with incremental increases in salinity in the range of 16-58 g L^{-1} (Figure 18). These data indicate that increasing salinity diminished the growth of *Nodularia* in the natural range commonly observed in the bay. These results are similar to the bioassay results presented in Marcarelli et al. (2006), where *Nodularia* biomass decreased at salinities >30-40g L^{-1}. In contrast to the response of *Nodularia* in bioassays, our salinity assay showed that overall algal levels, as measured by chlorophyll *a*, increased with rising salinity (Figure 18). Consequently, trophic status could still increase with increasing salinity, even though cyanobacteria decline (as indicated by phycocyanin levels in the June 29 experiment).

It is possible that due to genotypic variability the *Nodularia* in the Great Salt Lake has a higher salinity tolerance than *Nodularia* in the Baltic Sea. Another possibility is that the growth of Farmington Bay *Nodularia* actually peaks in the same salinity range as those found in the Baltic Sea (Moissander et al. 2002, Marcarelli et al. 2006), and the high concentrations we observed in higher salinity areas was due to advection and mixing of low-salinity water masses with more saline water to the north that had mixed with the intrusions from Gilbert Bay of Great Salt Lake.

Nutrients across the bay

Nutrients from municipal waste, diffuse pollution, and natural sources nourish the phytoplankton community in Farmington Bay. We observed mean total nitrogen (TN) and total phosphorus (TP) concentrations of 5.2 mg L^{-1} and 0.57 mg L^{-1}, respectively. These values are comparable to those found in previous years (Wurtsbaugh et al. 2012). The high levels of nitrogen we observed were weakly but significantly correlated to *Nodularia* in our study (Pearson's $r = 0.55$, $t = 3.425$, $df = 27$, p-value = 0.0020). Although our data indicates that total nitrogen was correlated with *Nodularia*, it is unclear if the high level of TN causes the *Nodularia* population to increase, or if high N-fixation rates of this species increases the TN concentration. Others have found no correlation between TN and *Nodularia*, but those surveys included data from outside the growing season, where nutrient cycling in the water column was likely different from our study due to the seasonality of biotic processes (Marcarelli et al. 2006, Wurtsbaugh et al. 2012, Marden et al. in prep.). TP was not correlated to *Nodularia* in our study. This is likely because *Nodularia* have the ability to collect and hold phosphorus through a process known as "luxury uptake", where this nutrient is held within *Nodularia* cells above the amount needed for growth and metabolism (Litchman et al. 2010). The high phosphorus concentrations found at the south end of the bay were likely from the waste water treatment works that discharge there, but we cannot rule out periodic releases of phosphorus from legacy sediments.

Our bioassay data indicate that phytoplankton in the bay (as measured by chlorophyll *a*) was limited primarily by nitrogen. This result is consistent with the results of Marcarelli et al. (2006) when compared to their 6-day long bioassays. However, they found that when the assays were allowed to continue for 30 days, nitrogen-fixation by cyanobacteria overcame the N limitation, and the phytoplankton communities became P-limited. Similarly, water column TN:TP ratios suggest that growth of phytoplankton in the south end of Farmington Bay may be nitrogen limited, with an increasing phosphorus limitation further to the north in the bay. This change may be due to fixation of atmospheric N_2 in the heterocysts of *Nodularia* (Marcarelli et al. 2006), and to sedimentation losses of P. Our bioassay data also indicate that cyanobacteria in the bay (as measured by phycocyanin) was stimulated by the addition of N or both +N+P, with lower phycocyanin concentrations found in experiments where only P was added.

Between 40-60% of nutrients entering Farmington Bay are derived from human waste sources (Meyers and Houston 2006). This preliminary analysis of P loading to the bay from municipal wastes alone is 2.6 g P m^{-2} yr^{-1} (Meyers and Houston 2006), well above the 0.1 mg P m^{-2} yr^{-1} estimated to cause "dangerous loading" in shallow freshwater lakes (Wetzel 2001). Using phosphorus input and outflow data for Farmington Bay presented in Meyers and Houston (2006) we determined that the sediments there are a sink for phosphorus, with over 60% of the incoming P loading from municipal wastes remaining in the bay and not being flushed to Gilbert Bay. However, if external loading was reduced, nutrients would likely diffuse out of legacy sediments during anoxic conditions (Mortimer 1941, Van Luijn et al. 1999). Estimates from other systems indicate that over a decade is required for a new equilibrium to be established once loading is decreased (Jeppesen et al. 2007). Limited work has been done to establish the N loading to the bay, but Gray (2012) showed that ammonia release from the sediments just upstream from the bay in Farmington Bay Waterfowl Management Area had diel cycles of ammonia. That study suggested that release of N from sediments may also occur during times of low dissolved oxygen.

Top-down and Bottom-up Controls on Phytoplankton

Sommer et al. (2012) tested models that assess the limits on phytoplankton growth in lakes and the ocean and found that many factors play into the balance of different functional groups of phytoplankton. They looked at classic models that had a simple suite of parameters to determine the controls on phytoplankton growth, which included the physical controls of light and temperature combined with grazing of zooplankton and nutrient limitation (Sommer et al. 1986). In addition to those parameters, the more recent evaluation found several other factors that might control the growth of phytoplankton (Sommer et al. 2012). Those factors included overwintering populations of grazing zooplankton and grazing by heterotrophic protists which emerge early in the growing season, parasitism effects on grazing zooplankton, the role of food quality in supporting grazing zooplankton populations, and phytoplankton reproductive strategies.

We found high densities of zooplankton that likely grazed huge amounts of phytoplankton and preyed upon other small organisms, including smaller zooplankton, bacteria, fungi, and protists. Lampert (1987) estimated that a *Daphnia* could filter 2-15 mL of the water column per day. Although the majority of the zooplankton observed in our study were not *Daphnia*, zooplankton in high enough concentrations likely filtered significant portions of the algae in Farmington Bay, but the high chlorophyll levels normally observed indicate that there was insufficient grazing pressure to create clear water conditions.

Recommendations for Future Research

The findings in this report help us to prioritize the direction of future study in Farmington Bay. Although we found high levels of *Nodularia* in the bay, we did not address potential adverse impacts to wildlife or the aquatic food chain. Future studies should focus on this topic. In order to determine if *Nodularia* and nodularin are actually impacting birds or aquatic life, we should focus on areas that birds typically congregate during the months when *Nodularia* is present. Our study focused on the open waters across the middle of the bay and migratory birds use this area at times, but shoreline areas might be more

likely areas for impacts because winds often push scums of cyanobacteria to the shore. It would be helpful to know if nodularin or other toxins are accumulating in sediments along these shorelines. This could be accomplished by collecting sediments during the most common bloom times (June) and testing for nodularin and other common toxins produced by cyanobacteria, including β-methyl-amino-L-alanine (BMAA). Once we determine what the concentration of key toxins are in the bay and what the legacy of those toxins is in surrounding sediments, relative risk models can be developed to compare the effect of cyanotoxins with other environmental contaminants such as metals and other pathogens.

The results of our study have also provided some guidance on future studies of the bay for the agencies charged with protecting Utah's natural resources. For the Utah Division of Water Quality's Great Salt Lake monitoring plan, at least one of the sample stations should be placed further south in the bay because conditions frequently were much different their than in the north. Researchers should look more closely at the ecosystem dynamics by using a phytoplankton ecology model that includes the inputs of grazing of algae by macrozooplankton, protists, parasitism, the microbial loop, release of different forms of nutrients from the sediments, and overwintering zooplankton populations. Because ammonia tends to stimulate cyanobacteria, and nitrate increases populations of diatoms and green algae (Blomqvist et al. 1994), the importance of loading and recycling of these two types of nitrogen needs to be assessed. We should also assess the loading of both N and P into the bay and explore other possible limitation of toxic cyanobacteria growth.

We should continue to develop our understanding of the conditions under which we get the most concentrated blooms of the toxic cyanobacteria *Nodularia*. We should also attempt to develop a further understanding of the top-down grazing pressures or bottom-up nutrient limitation approaches that might provide some control of the phytoplankton growth. Furthermore, we may want to consider options for increasing the salinity in the bay above that tolerated by *Nodularia* by making the Antelope Island causeway more permeable to water from Gilbert Bay. This latter option may provide the most cost-

effective solution, considering the limited resources available for implementing reasonable solutions, but may also produce some unexpected consequences. Overall, a collaborative approach to developing this understanding will lead to the best outcomes for all parties involved.

Some ideas for future research include developing better knowledge of the food web in the bay and its connection to the brine shrimp industry and human health. A better modeled food web would help us understand the dynamics controlling cyanobacteria and phytoplankton growth. We should also further develop the connection with nutrients and the brine shrimp industry and determine if the cyanotoxins adversely affect the brine shrimp in the open waters. We also need to develop a better understanding of the human health effects of blowing dust on communities close to the lake as more dry lake bed emerges. If drought conditions persist and water withdrawals from source rivers continue unabated these dust events may become more common. We need to conduct further studies to see if there is a link between the conditions in the bay and bird health or the health of the ecosystem components that support healthy migratory bird populations. This should include the possible link to avian botulism or other bird health issues (Murphy et al. 2000).

Once we understand the conditions that support the growth and persistence of toxic cyanobacteria in the bay, we will be able to better predict when blooms might occur. Research funding might also be well spent on developing our understanding of the conditions that are most likely to produce toxins and release them into the environment effecting wildlife and other aquatic organisms.

Conclusion

In summary, our observations indicate that there are periods when high concentrations of cyanobacteria and high levels of the liver toxin nodularin are present in the bay. These conditions may be more prevalent in the future with lower levels of the Great Salt Lake and less freshwater input reducing the effect of dilution. Although cyanobacteria react to changes in the physical parameters such as light, temperature and salinity, they also react to changes in availability of key resources needed for cell

building, such as nitrogen and phosphorus and grazing from herbivorous and omnivorous metazoans. There are both top-down and bottom-up effects on the size and structure of algal and metazoan populations.

Sustaining the importance of Farmington Bay is of international importance because the bay has been designated as a Western Hemisphere Shorebird Reserve Network Important Bird Area (WHSRN, Audubon Society 1991). In some ways nutrients benefit the ecosystem of Farmington Bay and the Great Salt Lake because they stimulate the food web for migratory birds and aquatic organisms. On the other hand, the cyanotoxins that have been found in Farmington Bay have been implicated in acute poisoning of dogs, birds and humans across the globe (Francis 1878, Nehring 1993, Mazur-Marzec et al. 2007, Simola et al. 2012, Drobac et al. 2013). Murphy et al. (2000, 2003) have also suggested that cyanotoxins may be related to outbreaks of avian botulism. More work is needed to definitively link these toxins with detriments to wildlife and the aquatic life in Farmington Bay and the Great Salt Lake, but the precautionary principle provides some impetus to continue evaluating the conditions in the bay, for the health of humans and our environment.

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Appendix A. Field parameters measured using a data sonde and sample locations during the 2012-2013 transects in Farmington Bay.

Date	Station	Identifier	Time	Latitude	Longitude	Depth Station (m)	Salinity (%)	Salinity ($g\ L^{-1}$)	Temperature °C (0.2 m)	Dissolved Oxygen (µg/L)	Secchi (m)
18-Jun-12	1	FB-1	12:20 PM	40.91867	-112.03187	0.3	2.6	25	25.7	8.2	>0.28
18-Jun-12	2	FB-2	11:48 AM	40.91867	-112.03187	0.8	3.4	34	25.6	15.5	0.4
18-Jun-12	3	FB-3	1:30 PM	40.93062	-112.09158	1.4	3.5	35	26.0	16.3	0.3
18-Jun-12	4	FB-4	2:13 PM	40.95892	-112.1087	1.5	3.5	35	28.1	20.4	0.3
18-Jun-12	5	FB-5	2:38 PM	40.98033	-112.11893	1.2	3.6	36	28.5	20.2	0.3
19-Jun-12	6	FB-6	10:47 AM	41.00329	-112.13969	1.6	4.8	49	20.3	5.5	0.4
19-Jun-12	7	FB-7	11:47 AM	41.01264	-112.15137	1.6	4.5	45	20.7	5.2	0.4
19-Jun-12	8	FB-8	12:29 PM	41.04402	-112.17076	1.6	4.5	45	21.5	4.4	0.3
19-Jun-12	9	FB-9	1:57 PM	41.05915	-112.18826	1.6	4.9	50	23.0	5.6	0.3
21-Sep-12	1	FB-1	9:40 AM	40.91867	-112.03187	0.3	0.5	3	14.5	1.4	0.2
21-Sep-12	2	FB-2	10:23 AM	40.91867	-112.03187	0.4	2.8	27	23.0	4.6	0.4
21-Sep-12	3	FB-3	10:41 AM	40.93062	-112.09158	0.7	2.5	24	21.3	1.2	0.5
21-Sep-12	4	FB-4	11:09 AM	40.95892	-112.1087	0.9	4.3	43	20.3	11.2	0.5
21-Sep-12	5	FB-5	11:43 AM	40.98033	-112.11893	0.8	4.9	43	20.3	12.3	0.4
21-Sep-12	6	FB-6	12:26 PM	41.00329	-112.13969	1.0	6.8	50	22.8	12.6	0.3
21-Sep-12	7	FB-7	1:00 PM	41.01264	-112.15137	0.8	6.2	71	22.4	12.3	0.4
21-Sep-12	8	FB-8	1:26 PM	41.04402	-112.17076	1.2	7.2	64	21.7	13.2	0.4
21-Sep-12	9	FB-9	1:55 PM	41.05915	-112.18826	1.3	7.4	76	22.2	12.1	0.3
3-May-13	1	FB-1	10:53 AM	40.91867	-112.03187	0.4	0.4	78	13.6	5.5	>0.44
3-May-13	2	FB-2	12:21 PM	40.91867	-112.03187	0.7	1.0	2	15.7	11.0	>0.65
3-May-13	3	FB-3	12:34 PM	40.93062	-112.09158	1.0	1.2	8	15.9	11.1	0.9
3-May-13	4	FB-4	1:35 PM	40.95892	-112.1087	1.1	1.5	10	16.5	10.1	0.8
3-May-13	5	FB-5	2:00 PM	40.98033	-112.11893	1.0	1.6	13	18.1	9.9	0.8
3-May-13	6	FB-6	2:30 PM	41.00329	-112.13969	1.0	1.6	14	18.2	8.6	0.9
3-May-13	7	FB-7	2:52 PM	41.01264	-112.15137	1.3	2.0	14	16.8	8.6	1.1
3-May-13	8	FB-8	3:45 PM	41.04402	-112.17076	1.4	2.5	24	16.1	5.5	1.1
3-May-13	9	FB-9	3:52 PM	41.05915	-112.18826	1.5	2.6	25	15.6	4.5	1.1
3-Jun-13	1	FB-1	1:55 PM	40.91867	-112.03187	0.5	0.2	1	22.9	5.3	>0.5
3-Jun-13	2	FB-2	1:33 PM	40.91867	-112.03187	0.7	0.6	4	22.6	15.4	0.2
3-Jun-13	3	FB-3	1:05 PM	40.93062	-112.09158	1.0	0.9	7	21.5	10.1	0.2
3-Jun-13	4	FB-4	12:54 PM	40.95892	-112.1087	1.1	1.4	12	21.1	11.4	0.1
3-Jun-13	5	FB-5	11:54 AM	40.98033	-112.11893	1.0	1.6	14	20.0	4.4	0.2
3-Jun-13	6	FB-6	11:29 AM	41.00329	-112.13969	1.0	2.3	22	18.8	4.3	0.2
3-Jun-13	7	FB-7	10:55 AM	41.01264	-112.15137	1.2	3.0	29	18.1	5.1	0.2
3-Jun-13	8	FB-8	10:05 AM	41.04402	-112.17076	1.5	0.3	0.5	18.3	3.7	0.3
3-Jun-13	9	FB-9	9:23 AM	41.05915	-112.18826	1.2	3.7	37	17.5	3.1	0.2
28-Jun-13	1	FB-1	9:44 AM	40.91867	-112.03187	0.2	0.2	5	25.0	2.7	>0.15
28-Jun-13	2	FB-2	10:19 AM	40.91867	-112.03187	0.4	0.6	6	26.6	4.2	0.4
28-Jun-13	3	FB-3	10:44 AM	40.93062	-112.09158	0.7	0.9	18	28.2	4.6	0.6
28-Jun-13	4	FB-4	11:30 AM	40.95892	-112.1087	0.9	1.4	25	27.8	6.1	0.6
28-Jun-13	5	FB-5	11:50 AM	40.98033	-112.11893	0.7	1.8	29	27.5	3.1	0.5
28-Jun-13	6	FB-6	1:00 PM	41.00329	-112.13969	0.8	2.3	35	28.4	7.8	0.4
28-Jun-13	7	FB-7	1:18 PM	41.01264	-112.15137	1.0	3.0	38	28.8	12.1	0.4
28-Jun-13	8	FB-8	1:57 PM	41.04402	-112.17076	1.2	3.3	40	26.9	4.9	0.6
28-Jun-13	9	FB-9	1:57 PM	41.05915	-112.18826	0.9	3.7	42			0.7

Appendix B. Database of laboratory results for nutrients, pigments, and isotopes

Identifier	Date	Chl (µg/L)	Phycocyanin (TFU)	Nodularin (µg/L)	NH4-N (mg/L)	NO3-N (mg/L)	Soluble reactive phosphorus (mg/L)	Total nitrogen (mg/L)	Total phosphorus (mg/L)	Organic nitrogen (mg/L)	Total inorganic nitrogen (mg/L)	Total phosphorus - soluble reactive phosphorus (mg/L)	Seston δ N15	Seston δ 13C
FB-1	18-Jun-12	175	2.53	3.7	0.15	0.04	0.04	4.85	0.50	4.66	0.19	0.46	5.42	-18.81
FB-2	18-Jun-12	165	4.65	3.3	0.01	0.04	0.02	5.69	0.32	5.64	0.05	0.29	3.78	-15.87
FB-3	18-Jun-12	125	7.95	10.8	0.15	0.05	0.03	5.38	0.27	5.18	0.20	0.25	3.02	-15.98
FB-4	18-Jun-12	141	7.04	4.1	0.15	0.06	0.03	4.51	0.21	4.30	0.21	0.19	2.08	-15.26
FB-5	18-Jun-12	124	6.24	3.5	0.16	0.06	0.02	5.43	0.26	5.21	0.22	0.23	2.51	-15.41
FB-6	19-Jun-12	150	4.49	2.8	0.23	0.05	0.03	5.48	0.27	5.20	0.27	0.24	3.48	-15.54
FB-7	19-Jun-12	175	4.98	6.9	0.20	0.04	0.02	5.40	0.30	5.16	0.24	0.27	3.31	-15.36
FB-8	19-Jun-12	205	4.45	11.2	0.23	0.05	0.03	5.89	0.41	5.61	0.28	0.39	3.27	-15.54
FB-9	19-Jun-12	171	4.24	5.5	0.31	0.05	0.03	5.56	0.31	5.20	0.35	0.28	3.17	-15.36
FB-1	21-Sep-12	128	1.53		0.06	0.02	0.41	2.93	0.69	2.85	0.08	0.28	NA	NA
FB-2	21-Sep-12	134	0.83		0.69	0.65	0.42	6.00	0.85	4.65	1.34	0.44	NA	NA
FB-3	21-Sep-12	167	0.64		0.14	0.32	0.19	4.76	0.64	4.30	0.46	0.45	NA	NA
FB-4	21-Sep-12	160	0.60		0.18	0.05	0.06	6.40	0.69	6.18	0.22	0.63	NA	NA
FB-5	21-Sep-12	130	0.59	1.0	0.20	0.03	0.06	6.19	0.64	5.96	0.22	0.58	NA	NA
FB-6	21-Sep-12	178	0.99		0.29	0.05	0.06	7.80	0.63	7.47	0.34	0.57	NA	NA
FB-7	21-Sep-12	114	1.01		0.24	0.06	0.04	6.42	0.53	6.13	0.30	0.49	NA	NA
FB-8	21-Sep-12	167	1.25		0.28	0.06	0.05	7.18	0.59	6.84	0.34	0.54	NA	NA
FB-9	21-Sep-12	161	1.58		1.20	1.08	0.11	7.69	0.25	5.41	2.28	0.14	NA	NA
FB-1	3-May-13	9	1.31		0.18	0.01	0.53	2.26	0.64	2.07	0.19	0.10	8.95	-23.75
FB-2	3-May-13	28	1.13	0.5	0.34	0.23	0.27	2.24	0.26	1.67	0.57	-0.01	10.67	-21.29
FB-3	3-May-13	29	1.17	0.6	0.60	0.20	0.15	3.79	0.44	2.99	0.80	0.28	10.69	-21.73
FB-4	3-May-13	27	1.26	0.3	0.23	0.04	0.06	2.78	0.23	2.52	0.27	0.17	10.33	-21.48
FB-5	3-May-13	33	1.01	0.2	0.15	0.01	0.05	3.39	0.31	3.23	0.16	0.26	10.18	-21.19
FB-6	3-May-13	14	1.15		0.24	0.01	0.03	3.35	0.28	3.11	0.24	0.25	9.42	-20.42
FB-7	3-May-13	17	0.93	0.2	0.28	0.01	0.02	3.35	0.28	3.07	0.29	0.26	8.56	-21.42
FB-8	3-May-13	6	0.88	0.8	0.18	0.01	0.02	3.00	0.21	2.82	0.19	0.19	8.18	-20.61
FB-9	3-May-13	6	0.93	0.5	0.20	0.01	0.03	3.08	0.22	2.88	0.21	0.20	8.16	-20.43
FB-1	3-Jun-13	19	1.15	1.2	0.22	0.04	0.59	1.60	0.69	1.33	0.27	0.10	9.26	-23.36
FB-2	3-Jun-13	224	6.02	12.9	0.33	0.03	0.26	5.37	0.91	5.01	0.36	0.65	6.95	-20.49
FB-3	3-Jun-13	267	17.60	69.4	0.53	0.09	0.02	7.20	0.85	6.57	0.63	0.83	5.94	-18.54
FB-4	3-Jun-13	175	17.80	68.0	0.57	0.01	0.01	7.11	0.67	6.52	0.59	0.66	5.65	-17.26
FB-5	3-Jun-13	193	21.10	52.0	0.64	0.00	0.01	7.32	0.58	6.67	0.65	0.57	4.78	-17.11
FB-6	3-Jun-13	131	15.40	43.1	0.75	0.11	0.01	6.83	0.51	5.97	0.86	0.50	3.96	-17.38
FB-7	3-Jun-13	116	15.70	31.1	0.73	0.17	0.01	5.33	0.35	4.43	0.89	0.34	3.90	-17.72
FB-8	3-Jun-13	122	13.30	30.0	1.16	0.14	0.01	6.32	0.45	5.02	1.30	0.43	4.26	-18.13
FB-9	3-Jun-13	146	16.90	31.7	0.91	0.24	0.02	6.70	0.46	5.55	1.15	0.44	3.59	-17.87
FB-1	28-Jun-13	45	1.37		0.50	0.04	3.36	4.15	3.50	3.60	0.55	0.14	NA	NA
FB-2	28-Jun-13	48	1.74		0.50	0.04	3.36	4.15	3.50	3.60	0.55	0.14	NA	NA
FB-3	28-Jun-13	54	1.83		0.09	0.01	0.01	5.77	0.54	5.67	0.10	0.53	NA	NA
FB-4	28-Jun-13	67	5.38		0.11	0.01	0.01	6.21	0.37	6.09	0.12	0.36	NA	NA
FB-5	28-Jun-13	78	2.21		0.16	0.02	0.02	6.78	0.45	6.61	0.17	0.43	5.35	-16.03
FB-6	28-Jun-13	118	3.05		0.13	0.01	0.01	6.47	0.34	6.32	0.15	0.33	4.36	-15.73
FB-7	28-Jun-13	85	5.60		0.06	0.01	0.01	6.48	0.36	6.41	0.07	0.35	3.36	-16.46
FB-8	28-Jun-13	39	3.16		0.14	0.01	0.01	4.91	0.23	4.76	0.15	0.22	3.49	-16.70
FB-9	28-Jun-13	47	4.28		0.05	0.01	0.01	6.06	0.29	5.99	0.07	0.28	3.10	-16.36

Appendix C. Database of phytoplankton densities measured in Farmington Bay on five dates in 2012-2013. The counts were done by Phycotech, Inc., St. Joseph, MI.

Identifier	Date	Zooplankton (individuals/L)	Zoop Biomass (µg/L)	Bacillariophyta Biovolume (µm/mL)	Chlorophyta Biovolume (µm/mL)	Chrysophyta Biovolume (µm/mL)	Cryptophyta Biovolume (µm/mL)	Cyanophyta Biovolume (µm/mL)	Euglenophyta Biovolume (µm/mL)	Haptophyta Biovolume (µm/mL)	Misc Algae (µm/mL)	Pyrrophyta Biovolume (µm/mL)	Tot. Phyto Biovolume (µm/mL)	Bacillariophyta (cells per mL)	Chlorophyta (cells per mL)	Chrysophyta (cells per mL)	Cryptophyta (cells per mL)	Cyanophyta (cells per mL)	Euglenophyta (cells per mL)	Haptophyta (cells per mL)	Misc Algae (cells per mL)	Pyrrhophyta (cells per mL)	Tot. Phyto (cells per mL)	Nodularia Biovolume (µm/mL)	Nodularia Concentration (cells per mL)	Dunalliela Biovolume (µm/mL)	Dunalliela Concentration (cells per mL)	Heterocysts per mL	Heterocysts per cell (ratio)
FB-1	18-Jun-12	258	1135	26498674	1541118	0	275529	33707	0	89506	0	354759	2294618	82999	23149	0	3105	51538	0	847	0	1129	162768	0	0	765531	12139	0	NA
FB-2	18-Jun-12	196	763	22957022	1712301	0	95785	74415866	0	0	0	214274	76438226	93105	22867	0	847	578821	0	0	0	565	695205	74210770	307363	222761	3105	28607	9%
FB-3	18-Jun-12	344	1802	53116012	4565783	0	766279	28243151	0	38420	0	0	287801999	118569	54556	0	1270	1571339	0	1270	0	0	1747004	282207633	1358169	1207162	16515	181665	13%
FB-4	18-Jun-12	112	423	19568321	574364	0	0	44781254	0	0	0	180927	45536545	86894	7602	0	0	297508	0	0	0	282	392287	44723225	197663	148999	988	13551	7%
FB-5	18-Jun-12	78	303	16245693	822231	0	136227	42072946	0	5123	0	106428	43142955	61250	6843	0	678	341100	0	169	847	339	411225	41982133	180494	204341	1355	13339	7%
FB-6	19-Jun-12	116	579	14439335	1658516	0	0	10700470	0	0	0	155384	12514370	69024	13381	0	0	307812	0	0	0	339	390557	10566434	51971	95785	508	2329	4%
FB-7	19-Jun-12	116	615	15889775	2571077	0	85142	14318703	0	0	0	340568	17315491	115605	41796	0	423	508647	0	0	0	847	667318	13976602	65319	170284	423	2964	5%
FB-8	19-Jun-12	31	321	23761593	6221738	0	0	27913121	0	0	0	0	34134859	145671	63519	0	0	559578	0	0	0	169	768768	27671171	135508	79821	423	8469	6%
FB-9	19-Jun-12	61	901	8691819	2447681	0	0	41487478	0	0	0	204341	44139499	81135	30489	0	0	607424	0	0	0	169	719218	41200245	201653	0	0	13043	6%
FB-1	21-Sep-12	53	2122193	305199	75682	3611440	182562	30864	0	54988	0	0	6382929	4235	10728	2258	106430	585707	282	0	847	0	710487	847	0	53214	1412	0	NA
FB-3	21-Sep-12	30	5311534	1449352	0	7095	37868	0	0	0	14390	148112	6968351	28054	18971	0	212	72877	0	0	212	423	120749	212	0	0	0	0	NA
FB-5	21-Sep-12	24	5284129	2242618	0	15420	1513663	0	0	0	0	1227268	10283097	35571	20467	0	20	194624	0	0	0	3529	254211	1880221	5505	0	0	423	8%
FB-7	21-Sep-12	0	5284129	2242618	0	15420	1513663	0	0	0	0	1227268	10283097	7854	110312	0	0	269102	0	10163	0	2329	399761	0	0	0	0	0	NA
FB-9	3-May-13	33	33	2730089	21919744	0	0	6708764	0	742794	0	2043410	34144802	22020	268221	0	0	1197165	0	24561	0	3388	1515355	0	0	0	0	0	NA
FB-1	3-May-13	11	11	1892887	929947	115261	14190	147311	0	0	0	0	2971587	20750	18209	3811	423	174581	0	0	0	0	217774	0	0	0	0	988	0	NA
FB-3	3-May-13	18	18	2311113	300058	2478	8514	4310558	0	0	0	0	5399304	27086	2244	127	42	45132	3	0	85	0	74719	2890592	14009	0	0	1534	11%
FB-5	3-May-13	14	14	6073486	189993	0	0	924595	0	0	0	0	6768670	32797	1306	0	0	24100	0	0	0	0	58203	612370	2981	0	0	271	9%
FB-7	3-May-13	41	41	2861057	243872	479	0	2717365	180842	0	0	0	4937294	19107	796	34	0	16940	102	0	0	0	36979	1798055	8779	0	0	681	8%
FB-9	3-Jun-13	19	19	1107037	170773	0	0	536528	0	0	0	0	1526451	10267	271	0	0	5564	0	0	0	0	16102	356832	1737	0	0	157	9%
FB-1	3-Jun-13	12	12	844288	1104813	25700	20694	160748	125585	140875	0	3427	2426130	4658	52028	20	282	153742	141	4658	0	20	215551	45232	225	0	0	0	0%
FB-3	3-Jun-13	52	52	11930196	3262742	0	104765	79941523	0	461045	0	0	9570070	89632	222212	0	1270	710365	0	15245	0	0	1038723	7973641	393027	0	0	14221	4%
FB-5	3-Jun-13	39	39	930243	774217	41507	3548	10764983	0	38420	0	0	10943775	5964	33361	106	106	642059	0	1270	0	0	682866	10759882	527297	0	0	31442	6%
FB-7	3-Jun-13	34	34	1385403	195561	0	9978	5632531	0	51227	0	0	5796747	9422	2329	0	106	405875	0	1694	0	0	419426	5626124	273249	0	0	13318	5%
FB-9	28-Jun-13	80	80	2570285	242542	0	0	5327037	0	43909	0	0	5612711	17023	4065	0	0	302931	0	1452	0	0	325471	5325806	257007	0	0	22020	9%
FB-1	28-Jun-13	46	46	1608038	31669	0	4730	32343	0	0	106241	0	1762635	847	692	0	0	16766	0	0	1397	0	19844	0	0	0	0	0	NA
FB-3	28-Jun-13	79	79	12671050	539975	4989	4730	8385131	0	0	0	57944	18234758	36813	2400	353	141	45254	0	0	0	71	85031	5140898	25147	0	0	1759	7%
FB-5	28-Jun-13	54	54	10348841	1132049	11352	0	7784524	0	0	0	0	16050036	36813	2400	353	141	45254	0	0	0	71	85031	5182813	25229	0	0	2283	9%
FB-7	28-Jun-13	32	32	3377214	3292471		0	9849155	0	0	0	66517	70901161	36813	2400	353	141	45254	0	0	0	71	85031	6560963	319345	0	0	29031	9%
FB-9	28-Jun-13		1243189	2520050	3991	0	77412037	0	0	0	0	25543	54026492	12446	6259	0	42	254277	0	0	0	42	273066	51272456	250365	0	0	19347	8%

CHAPTER 2. METALS AND METALLOIDS IN FARMINGTON BAY

Wayne A. Wurtsbaugh and Eric McCulley

Summary

To assess how contaminants changed along the north-south axis of Farmington Bay, metals (Cu, Pb, Cd, Hg, MeHg) and metalloids (Se, As) were sampled three times at five stations in Farmington Bay between May and June, 2013. On all three dates there was a strong salinity gradient from the south where river and wastewaters are discharged, to the north where exchanges with hypersaline Gilbert Bay increased the salinity to 26-43 g/L. Copper, lead and mercury concentrations were highest in the southern part of the bay near the discharge of water from the EPA Superfund site, the Northwest Oil drain. Concentrations at these sites were above levels of concern for the protection of aquatic organisms. However, concentrations of these pollutants decreased 2-5 fold at stations in the north. In contrast, concentrations of the metalloids, selenium and arsenic, were highest at the northern stations, perhaps as a consequence of increased mixing of Gilbert Bay water from an intruding salt wedge. Cadmium and methyl mercury concentrations showed less distinctive trends along the salinity gradient in the bay. Titanium concentrations were usually below levels of detection so that spatial trends could not be evaluated. The study documented that monitoring of contaminants in the bay should be done both in the north and south, particularly because bird use is highest in the southern area where some contaminant levels were highest.

Northwest Oil Drain and petroleum refineries in northern Salt Lake City.

Introduction

Farmington Bay is located in the southeast corner of the Great Salt Lake near the metropolitan Salt Lake City. At most lake levels, it is largely separated from the main lake by an automobile causeway connecting the mainland to the northern tip of Antelope Island. Inflows to the lake include Farmington Creek and the Jordan River. However, flows of the later are routed through artificial wetlands or partially diverted via the Goggin Drain to Gilbert Bay. Bi-directional flows between the bay and main lake (Gilbert Bay) is primarily via a 10.3-m wide breach in the Antelope Island Causeway. The inflow of dense, high-salinity water from Gilbert Bay causes a salt wedge, or deep-brine layer to form in the southern half of Farmington Bay. This layer is relatively stable, and decomposing organic matter results in anoxia and high concentrations of toxic hydrogen sulfide (Wurtsbaugh and Marcarelli 2004) below a depth of approximately 1 m.

There is usually a strong salinity gradient in the bay, ranging from freshwaters that support fish in the south, to higher salinities in the north due to interchange of water with Gilbert Bay. Discharges from secondary-level wastewater treatment plants constitute approximately 50% of total flows into Farmington Bay (Meyers and Houston 2006). A part of the inflow is via the Northwest Oil Drain/Sewage Canal that enters at the south end of the bay. The Northwest Oil Drain is a Superfund Cleanup Site due to contamination with metals and petroleum wastes (The Forrester Group 2001).

The bay is very shallow with a mean depth of <0.5 m, depending on lake level. During our study station depths ranged from 0.2-0.5 m at the southernmost location, to 1.5 m in the north (see Figure 1 in Chapter 1). The playas and the shallow littoral areas of the bay are used extensively by shorebirds and waterfowl (Aldrich and Paul 2002). Because of the potential contamination of the bay by the Oil Drain and sewage discharges, there is concern that the bird community, and potentially the fish community, is exposed to high levels of metals. Several studies have examined heavy metal concentrations in the sediments, particularly near the discharge of the Northwest Oil Drain, and found relatively high levels of

copper, lead and mercury (Sorensen and others 1988, Waddell et al. 2009, Wurtsbaugh 2012). However, the spatial extent of the high metal concentrations is not well known. Consequently, in concert with the *Nodularia* surveys discussed in Chapter 1, we analyzed concentrations of metals and metalloids in the water and in the biota along a transect running the length of the bay.

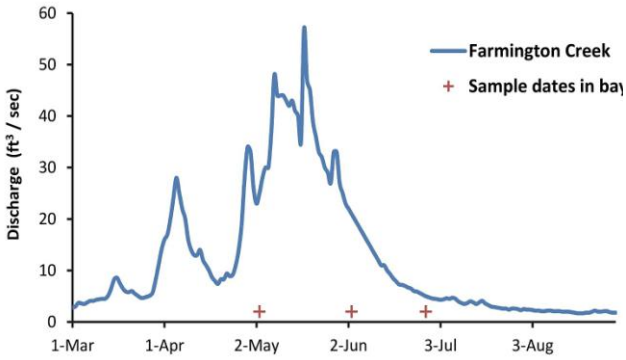

Figure 1. Discharge of Farmington Bay Creek, as an index of flows into Farmington Bay during the sampling period in 2013.

Methods

Water samples were collected at Stations 1, 3, 5, 7 and 9 during the 3 May, 3 June and 28 June, 2013 surveys. These dates spanned the early spring runoff to the beginning of base flows into Farmington Bay (Figure 1). Pre-cleaned bottles for the metal analyses were provided by Brooks Rand, Inc., Seattle, WA. These were filled with water from depths of 0.2 m and stored in ice chests before being sent back for analyses. Zooplankton for total mercury and selenium analysis were collected with horizontal tows of a 153-µm mesh net. Species composition of the zooplankton is discussed in Chapter 1. The samples were chilled and sent to Brooks Rand Laboratory for analyses. Salinities were measured with a refractometer on samples collected at a depth of 0.2 m. Refractometer units (%; X) were converted to units of grams of salt per liter using the empirical equation of W. Gwynn (unpublished data):

$$g/L = 0.0816*X^2 + 9.9633*X - 0.4353$$

The proportion of Gilbert Bay water that had mixed into Farmington Bay water was calculated using a mixing model assuming that inflow water had a salinity of 1 g/L and the Gilbert Bay water had a salinity of 145 g/L.

Arsenic (As), cadmium (Cd), copper (Cu), lead (Pb), selenium (Se) and titanium (Ti) in water were analyzed by Brooks Rand using pre-concentration and inductively coupled plasma-mass spectrometry following EPA procedure 1640 RP. Methyl mercury was analyzed by EPA procedure 1630 using distillation, aqueous ethylation, purge and trap, and cold vapor atomic fluorescence. Total mercury was analyzed with EPA procedure 1631, by oxidation, purge and trap, and cold vapor atomic fluorescence spectrometry. The zooplankton tissue samples were dried to a constant weight and then analyzed for selenium with EPA method 1638 DRC, and for mercury utilizing EPA procedure 1631 following acid digestion and BrCl oxidation. Some high-salinity water samples were diluted with deionized water prior to analysis. This caused the detection limits to be increased in proportion to the dilution (Table 1).

Table 1. Minimum detection limits for metals and metalloids analyzed by Brooks Rand Laboratories.

Metal	Media	Minimum detection limit	Units
Arsenic	water	0.100 - 0.500	µg/L
Cadmium	water	0.012 - 0.060	µg/L
Copper	water	0.040 - 0.200	µg/L
Lead	water	0.013 - 0.065	µg/L
Selenium	water	0.070 - 0.350	µg/L
Titanium	water	0.002 - 0.010	µg/L
Methyl mercury	water	0.020 - 0.101	ng/L
Total mercury	water	0.150 - 0.760	ng/L
Selenium	zooplankton	0.060 - 0.260	µg/g
Total mercury	zooplankton	0.300 - 3.330	ng/L

Although the Great Salt Lake has only one numeric criteria (for selenium) for contaminants in water, here we have provided the EPA's Criterion Continuous Concentration (CCC), which is an estimate of the highest concentration of a material in surface water to which an aquatic community can be exposed indefinitely without resulting in an unacceptable effect (EPA 2006). In most cases we used CCC values for fresh water, but when these were not available we substituted other values in order to provide some idea of the potential effects of the metals on the ecosystem. Criteria for mercury and selenium in zooplankton were taken from the avian dietary effect thresholds listed in Waddell et al. (2009).

Results

Background conditions—On all sample dates there was a strong salinity gradient ranging from 2-7 g/L at the south end of the bay (Station 1) to 26-43 g/L at the north end (Figure 1A). During the late June transect that was done after spring runoff, salinities were higher at all stations and reached 43 g/L at Station 9. As expected, estimated proportions of Gilbert Bay water in Farmington Bay were highest at the north end, and reached 29% at Station 9 during the 28 June transect (Figure 1B).

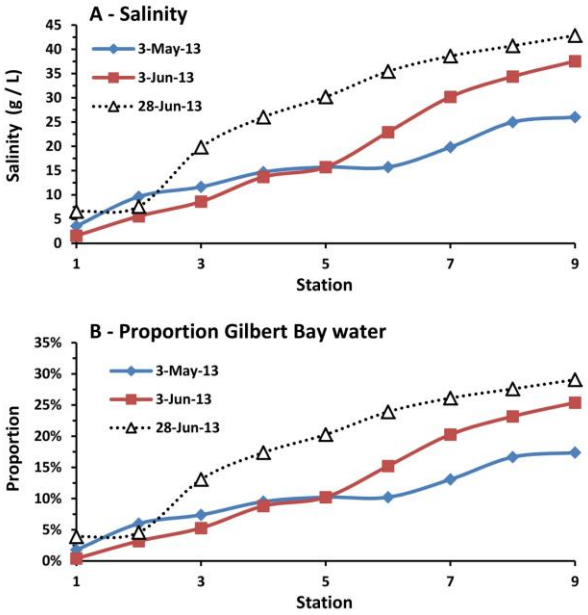

Figure 2. A. Salinities at all 9 stations in Farmington Bay on three sampling dates. B. Estimated proportions of Gilbert Bay water that had mixed with Farmington Bay water at the 9 stations.

Measurements of pH varied from 8.1 to 9.3 during the study. The lowest pHs were at Station 1 (8.1-8.7), and average 9.1 at the other stations. However, diel variations driven by changes in photosynthesis are considerable in hypereutrophic Farmington Bay (Wurtsbaugh 2011), so these daytime values are quite likely higher than the nighttime pH values.

Water temperatures during the transects varied substantially:

3 May 2013	14 – 18 °C
3 June 2013	18 – 23 °C
28 June 2013	25 – 29 °C

Although there were considerable temperature differences between stations on a given date, this may have been due to the northernmost stations being collected earlier in the morning before there was substantial daytime heating.

***Metal and metalloid concentrations in water*—**The metalloids, selenium and arsenic, were relatively constant across the bay (selenium; Figure 3A) or tended to increase at the northern stations (arsenic; Figure 3B). Selenium concentrations in Farmington Bay water ranged from 0.33 to 0.55 µg/L, and were well below the EPA Criterion Constant Concentration (CCC) of 5 µg/L. Arsenic concentrations ranged from 10-21 µg/L, and were also well below their CCC level of 150 µg/L. Concentrations of all constituents are given in Appendix I.

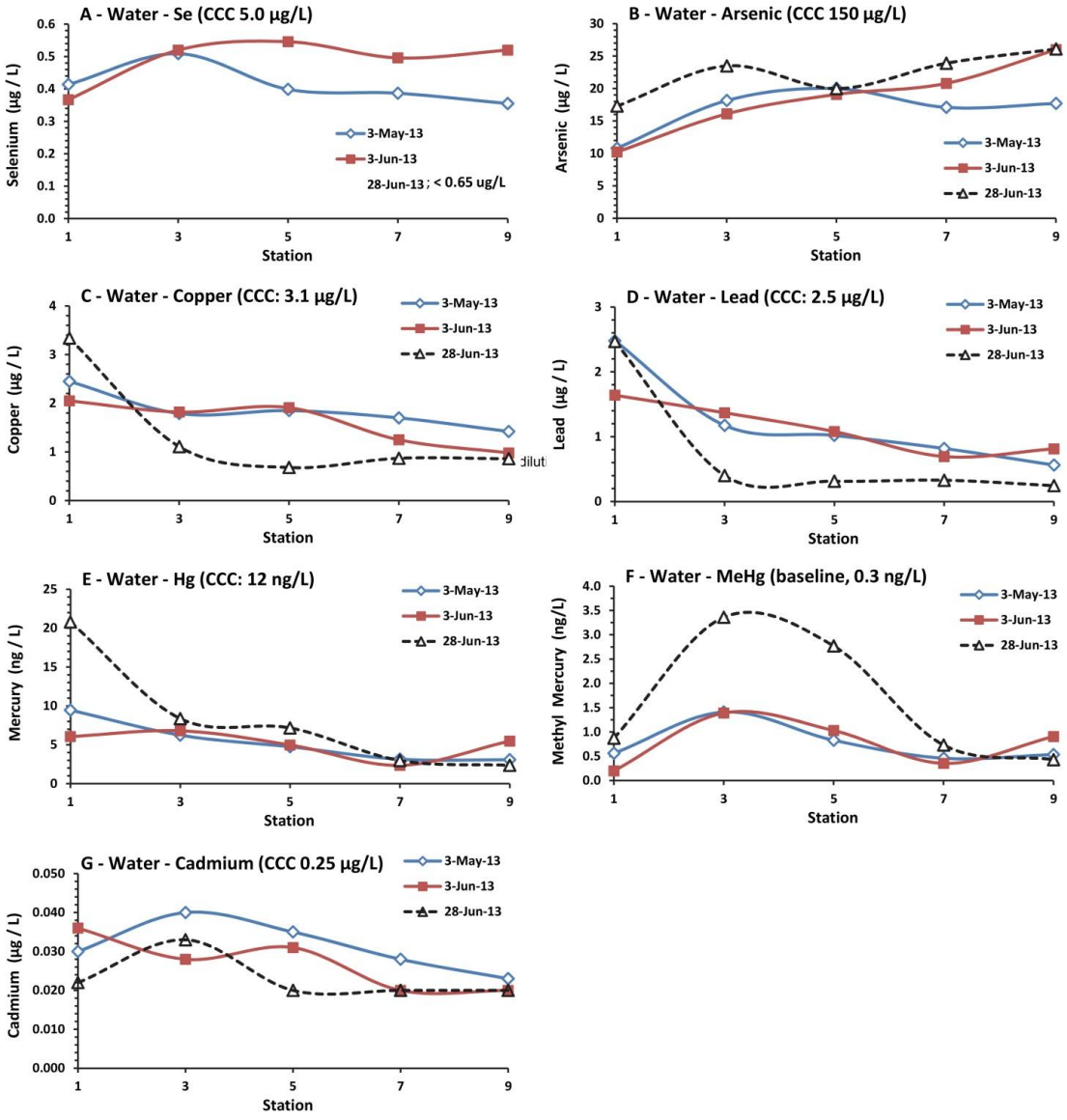

Figure 3. Total metal concentrations in lake water collected at 0.2 m at five stations in Farmington Bay on three dates in 2013. The EPA's Criteria Continuous Concentration (CCC) for fresh waters is given for each metal, except for copper, for which the marine CCC was used. Concentrations below the CCC reference level should provide adequate protection for aquatic organisms.

Copper, lead, mercury and cadmium levels in water were usually highest at the south end of Farmington Bay (Stations 1 or 3), and lowest at the northern end (Station 7 or 9) (Figures 3C-G). Copper and lead showed particularly strong gradients, with concentrations 2-3 times higher in the south than in the north (Figure 3C, D). Concentrations of both of these metals at Station 1were above their respective

CCCs on one or more dates. Total mercury at Station 1 was also above its CCC on the 28 June, 2013 sampling date (Figure 3E). Methyl mercury concentrations had a somewhat different pattern than total mercury, with concentrations peaking at Station 3, and decreasing both towards the south and north (Figure 3F). A CCC for methyl mercury has not been issued for this metal. Nevertheless, concentrations at nearly all stations and dates were considerably above the World's baseline background concentration of 0.3 ng/L (Gray and Hines 2009).

Cadmium also peaked at Station 3 on two dates, but overall the differences across the bay were less distinctive for this metal (Figure 3G). Cadmium concentrations in Farmington were approximately 10-fold less than its CCC. Titanium was only above levels of detection at Station 1 on 3 June and 28 June, with respective concentrations of 0.016 and 0.012 µg/L. All other samples were less than the detection levels which ranged from 0.002 - 0.010 µg/L, depending on the dilution used by the analytical laboratory.

Concentrations of copper, lead, cadmium and total mercury were negatively correlated with salinities at the stations where they were collected (Figure 4A, B). For example, copper concentrations were near 2.5 µg/L at salinities < 5 g/L, but declined to 0.9 µg/L at salinities near 40 g/L. Arsenic concentrations showed the opposite pattern, increasing from near 10 µg/L at salinities <5 g/L, to over 25 µg/L at the highest salinities

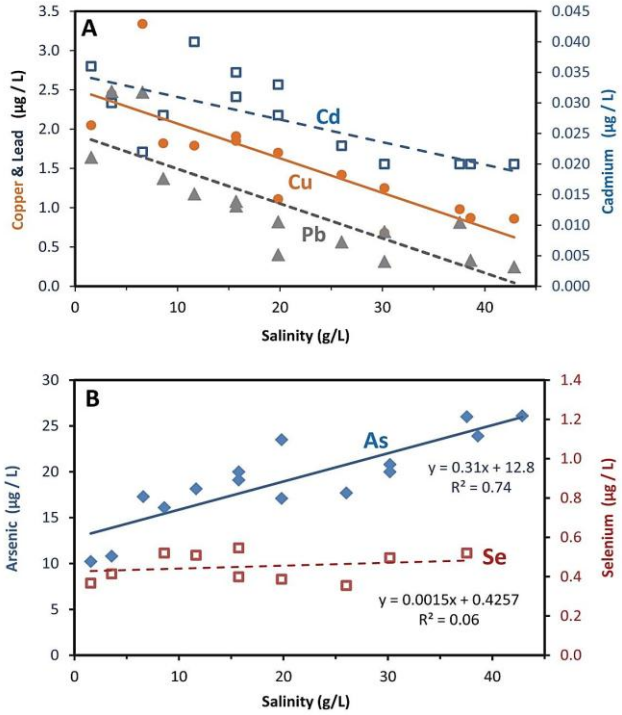

Figure 4. Relationship between salinity and concentrations of metals collected at five stations in Farmington Bay on three dates in 2013.

(Figure 4C). Methyl mercury and selenium concentrations were not correlated with salinities (Figure 4B, C).

Selenium & mercury in zooplankton

There were no strong spatial patterns in concentrations of selenium and mercury along the north-south transects in Farmington Bay (Figure 5). However, selenium concentrations tended to increase towards the north, and mercury concentrations in the zooplankton were highest in the south at Stations 3 or 1. Concentrations of Hg and Se on each date are given in Appendix II.

Concentrations of selenium and mercury in the zooplankton were significantly correlated with concentrations in the water (Figure 6). Selenium concentrations in the zooplankton increased approximately five-fold as concentrations in the water increased from 0.35 to 0.55 µg/L. However, relatively few data points were available for this analysis. Mercury concentrations in the zooplankton increased approximately three-fold as methyl mercury concentrations in the water increased from 0.2 to 3.5 ng/L (Figure 6B). However, the significant relationship was driven largely by two high points, indicating that the correlation should be treated cautiously until more data are available. Mercury concentrations in the zooplankton were not significantly correlated with total mercury concentrations in the water ($p = 0.19$).

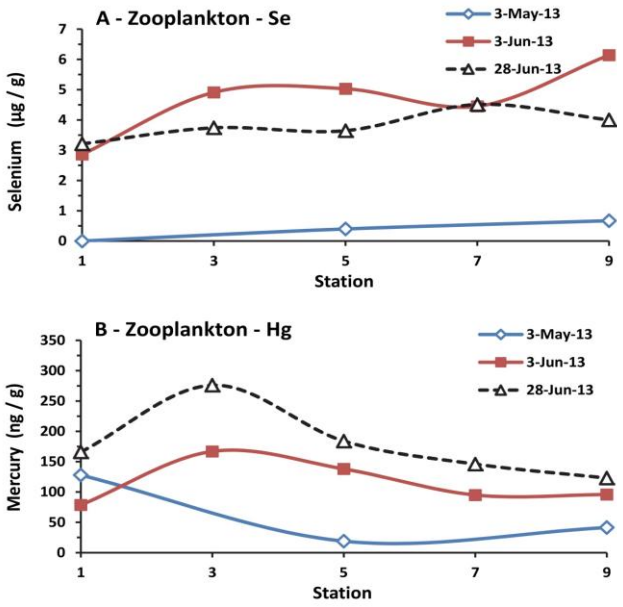

Figure 5. Concentrations of selenium (A) and mercury (B) in zooplankton collected along transects in Farmington Bay on three dates in 2013.

Discussion

Metal and metalloid concentrations measured in the zooplankton, and particularly in the water, had strong spatial gradients along the north-south axis of Farmington Bay but different moieties behaved differently. Arsenic, and to a certain extent, selenium, were higher at the north end of Farmington Bay. For arsenic, this may simply be a consequence of having a higher proportion of Gilbert Bay water mixed into the bay water, as arsenic concentrations in Gilbert are high (~150 ug/L; Sturm 1980). Selenium concentrations in the water of Gilbert Bay (Byron et al. 2011) are also somewhat higher (0.75 µg/L) than the mean concentrations measured in Farmington Bay (0.45 µg/L), so that mixing of water from the main lake could also increase concentrations of this metalloid.

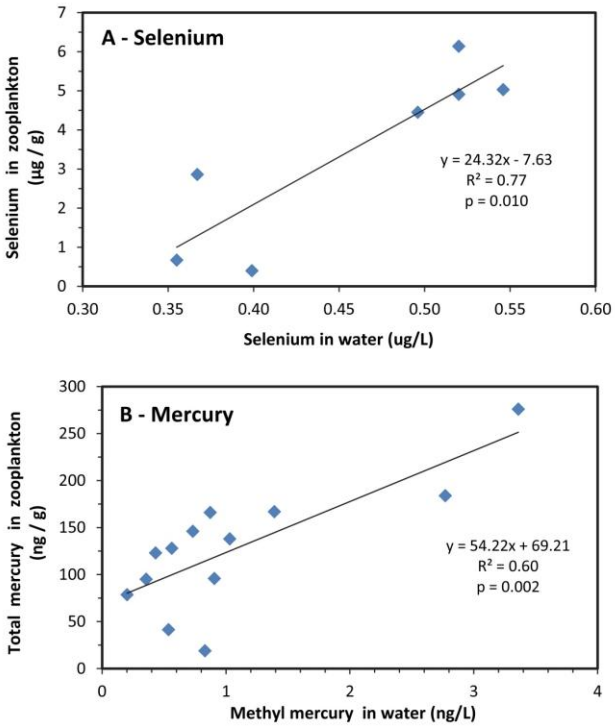

Figure 6. Relationships between selenium (A) and methyl mercury (B) in the water, and concentrations in zooplankton sampled on three dates at stations in Farmington Bay.

In contrast to the metalloids, concentrations of three of the heavy metals (Cu, Pb, Hg), decreased from the south to the north. Concentrations were particularly high at Station 1, which was located ~500 m from the discharge of the Northwest Oil Drain (Sewage Canal). Also note that during our study Station 1 was located in a broad, shallow channel largely separated from the main bay (See Figure 1, Chapter 1), so that waters there were fresher and more characteristic of the Jordan River and wastewater effluents discharging there than were stations further north. Decreases of copper, lead and mercury from the south to the north, could be due, in part, to dilution by increasing proportions of Gilbert Bay water to the north. Precipitation of these metals with increasing pH in the north is also possible, as metal solubility decreases

with increases in pH (Stumm and Morgan 1981). Releases of hydrogen sulfides from the northern deep brine layer and/or sediments during wind events could also contribute to the decline of metals in the north, as metal sulfides are also quite insoluble (Stumm and Morgan 1981). We also caution that although it seems likely that the gradients in concentrations are a consequence of the sources from the Northwest Oil Drain and Gilbert Bay seem likely, it is also possible that the depth gradient from the south (0.2 – 0.5 m) to the north (~1.5 m) could have influenced concentrations in overlying water. Consequently, further study will be required to determine the cause(s) of the north-south gradients.

Other studies have also reported higher concentrations of metals in the southern part of Farmington Bay near the Northwest Oil Drain (Sorensen and others 1988, Waddell et al. 2009, Wurtsbaugh 2012). A recent study of metals in Farmington Bay also noted high concentrations in the sediments in the south, but concentrations of most metals in the benthic invertebrates were highest at a station close to our Station 3 (unpublished data of C. Richards and W. Wurtsbaugh). This pattern was similar to what we observed for mercury in the zooplankton. More detailed sampling of the benthic invertebrates and zooplankton will be required to confirm if this is a general pattern.

The Utah Division of Water Quality currently samples water quality parameters in Farmington Bay only in the north near our Station 9. Sampling only in the north likely provides a biased indication of metal concentrations, many of which were higher in the southern part of the bay. This is particularly important because densities of wading birds are highest in the very shallow waters in the southern part of the bay (personal observation). Although concentrations of most of the metals were below levels of concern at most stations in Farmington Bay, levels in the far south approached or exceeded the EPA's Criterion Continuous Concentrations for copper, lead and mercury. Consequently, we suggest that at least periodic measurements of metals and other contaminants be made throughout the bay in order to determine whether birds and other aquatic wildlife are threatened. An additional issue is that salinities in the southern part of the bay are low enough so that freshwater fish are present. Although there is

currently no fishery there, piscivorous birds such as pelicans and eagles likely feed on carp or other fishes, so that there is a potential threat of biomagnification of metals in the food web. Consequently, contaminants in the fish community in the bay needs to be determined.

Acknowledgements

Leland Meyers and Dave Barnes from the Central Davis Sewer District, and Suzan Tahir from the Division of Water Quality provided airboat support and helped with the sampling. Brian Barnes assisted in the field and laboratory. Funding for the research was provided by the Utah Division of Water Quality and the Utah Department of Forestry, Fire and State Lands.

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Appendix I. Concentrations of metals (cadmium, copper, mercury, methyl mercury, lead) and the metalloids (arsenic and selenium) in water collected from five stations in Farmington Bay during 2013. ND – Below level of detection.

	As ($\mu g\ L^{-1}$)	**Cd** ($\mu g\ L^{-1}$)	**Cu** ($\mu g\ L^{-1}$)	**Hg** ($ng\ L^{-1}$)	**MeHg** ($ng\ L^{-1}$)	**Pb** ($\mu g\ L^{-1}$)	**Se** ($\mu g\ L^{-1}$)	**Ti** ($\mu g\ L^{-1}$)
Station				**3-May-13**				
1	10.8	0.030	2.45	9.46	0.56	2.48	0.41	ND
3	18.2	0.040	1.79	6.24	1.41	1.18	0.51	ND
5	20.0	0.035	1.85	4.75	0.83	1.02	0.40	ND
7	17.1	0.028	1.70	3.15	0.46	0.82	0.39	ND
9	17.7	0.023	1.42	3.08	0.54	0.56	0.36	ND
				3-Jun-13				
1	10.2	0.036	2.05	6.06	0.20	1.64	0.37	0.016
3	16.1	0.028	1.82	6.80	1.39	1.37	0.52	ND
5	19.1	0.031	1.91	4.98	1.03	1.08	0.55	ND
7	20.8	0.020	1.25	2.36	0.36	0.70	0.50	ND
9	26.0	0.020	0.98	5.48	0.91	0.81	0.52	ND
				28-Jun-13				
1	17.3	0.022	3.34	20.80	0.87	2.47	ND	0.012
3	23.5	0.033	1.11	8.37	3.36	0.40	ND	ND
5	20.0	0.020	0.68	7.17	2.77	0.32	ND	ND
7	23.9	0.020	0.87	2.98	0.73	0.33	ND	ND
9	26.1	0.020	0.86	2.36	0.43	0.25	ND	ND

Appendix II. Concentrations of total mercury and selenium in zooplankton collected at 3-5 stations in Farmington Bay on three dates. Concentrations are based on dry weights of the zooplankton. ND – Below levels of detection.

	Mercury ($ng\ g^{-1}$)	**Selenium** ($\mu g\ g^{-1}$)
Station	**3-May-13**	
1	128.0	ND
5	18.9	0.40
9	41.4	0.67
	3-Jun-13	
1	78.6	2.86
3	166.9	4.91
5	138.0	5.03
7	95.0	4.45
9	95.8	6.14
	28-Jun-13	
1	166.0	3.21
3	276.0	3.74
5	183.9	3.65
7	146.0	4.51
9	123.0	4.00

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CHAPTER 3. THE EFFECTS OF SALINITY ON PLANKTON AND BENTHIC COMMUNITIES IN THE GREAT SALT LAKE, UTAH, USA: A MICROCOSM EXPERIMENT

Brian D. Barnes and Wayne A. Wurtsbaugh

Summary—Saline lakes change in size and salinity due to natural climate variability and especially from inflow diversions, which threaten life in these waters. We conducted a microcosm experiment in 12-L containers using seed organisms from the Great Salt Lake to determine how salinities ranging from 10-275 g/L influenced the ecosystem (Figure I). In the 30-day experiment, brine shrimp (*Artemia franciscana*) were nearly absent in salinities of less than 10 g/L and greater than 225 g/L. Additionally, as salinities increased from 75 to 225 g/L, adult *Artemia* final weights decreased from 690 to 290 mg/individual and their total biomass decreased four-fold (Figure II A). Copepod and rotifer biomasses were negligible at salinities >50 g/L. Brine fly larval (*Ephydra gracilis*) individual weights decreased from 1.1 mg to 0.6 mg as salinity increased from 50 to 250 g/L, with a corresponding decrease in population biomass (Figure II B). When *Artemia* and other grazers were abundant at salinities <200 g/L phytoplankton chlorophyll levels were low (mean 4.0 µg/L), but when grazing rates declined at higher salinities, mean phytoplankton chlorophyll increased to 128 µg/L. Mean periphyton chlorophyll levels showed the reverse pattern, with 1.78 µg/cm^2 at salinities less than 200 g/L and only 0.05 µg/cm^2 at higher salinities (Figure II C). Total nitrogen concentrations decreased markedly over the course of the experiment, particularly at low salinities, whereas total phosphorus concentrations remained stable, resulting in final Redfield ratios indicative of algal nitrogen limitation. The mesocosm experiment demonstrated the strong influence of salinity on the ecosystem, and highlighted the decreasing biomass of brine shrimp as salinities increase. Additional planned diversions of water from the lake would further increase salinities and likely reduce the production of the important food organisms for birds that utilize the lake.

Figure I. Microcosms used to test the influence of salinity on the biotic community of the Great Salt Lake.

*Derived from a manuscript in the Canadian Journal of Fisheries and Aquatic Sciences (Barnes and Wurtsbaugh (in press).

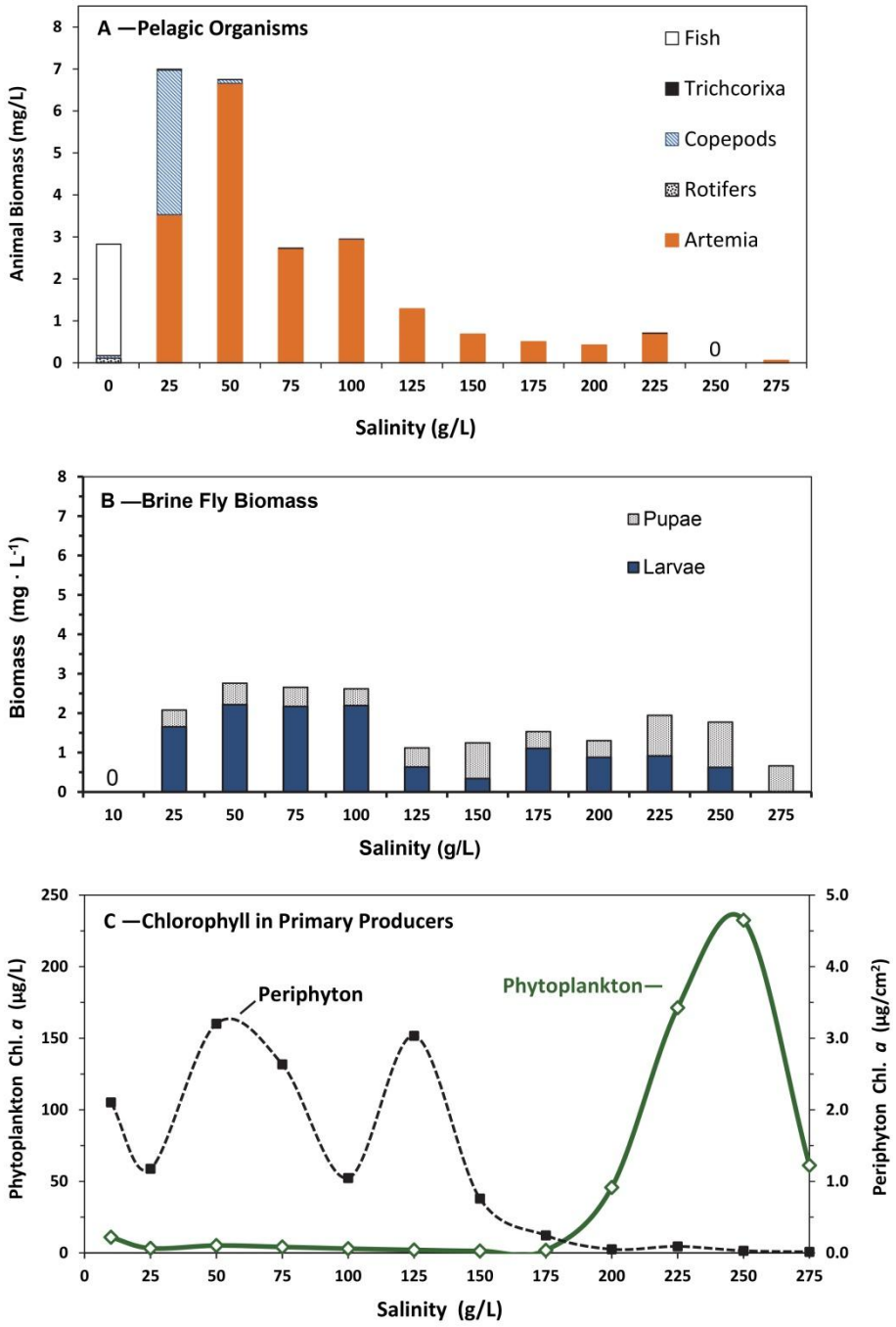

Figure II. A. Response of zooplankton and fish to twelve salinity treatments in a 30-day microcosm experiment. B. Response of benthic organisms to the salinity gradient. Brine fly larvae and pupae were the only surviving benthic organisms. C. Algal abundance measured as chlorophyll *a* in the phytoplankton and periphyton at the end of the 30 day experiment.

Introduction

Saline lakes represent 45% of the total inland lake volume in the world (van der Leeden et al. 1990). Low salinity (<30 g L^{-1}) lakes have fish and a diversity of plankton and benthic invertebrates, but with increasing salinities diversity is dramatically reduced. The primary physiological cost that limits production and survival of aquatic organisms in saline systems is osmoregulation, which eliminates many salt-intolerant organisms from hypersaline conditions. Changes in salinity can further affect food webs through competition and predation (Williams 1998). For example, when fish are present, many large, vulnerable zooplankton and many benthic invertebrates are eliminated (Hammer 1986). Invertebrate predators are also important in regulating community structure. For example, water boatmen, *Tichocorixa verticalis* (corixids) are often abundant at salinities <90 g L^{-1}, and vulnerable prey such as *Artemia franciscana* (brine shrimp) are eliminated by these predators at these lower salinities. However, *Artemia* are resilient osmoregulators and when salinities rise above levels where *T. verticalis* are able to survive, *Artemia* populations flourish (Wurtsbaugh and Berry 1990; Wurtsbaugh 1992). These constraints on the biota have been described by Herbst (1988) as the *intermediate salinity hypothesis*, where the abundances of salt-tolerant organisms are constrained by predators at low salinities, and by osmotic stress at high salinities.

Saline lakes naturally fluctuate in both size and salinity due to natural changes in wet and drought cycles. These changes have direct effects on the biota that populate saline lakes. In addition to natural changes, many saline lakes have been undergone anthropogenic modifications, the most universal being water diversion for agricultural, industrial, and urban uses (Williams 2001; Jellison et al. 2008). The desiccation of the Aral Sea in central Asia and the more recent drying of Lake Urmia (Iran) are examples of the most aggressive diversions of water for agriculture (Micklin 2007; Lotfi and Moser 2012). Water diversions and lake evaporation have greatly increased the salinity of these two lakes, leading to the loss of higher organisms such as zooplankton and fish.

Considerable observational and experimental data exists on the salinity-induced changes to the aquatic communities of salt lakes. However, these analyses have frequently only addressed a portion of the potential salinity range in these systems. For example, Carpelan (1957) and Larson and Belovsky (2013) used observational and experimental approaches to investigate how salinity influenced community structure, but only over the range of 25-150 g L^{-1}. In the Great Salt Lake (USA), Stephens (1990) and Wurtsbaugh (1992) reviewed how salinity has influenced the community structure and function, but they also did not address the full range of salinities that are possible in this ecosystem (0-330 g L^{-1}).

The Great Salt Lake, Utah (USA) is a terminal lake in the Great Basin of North America (Fig. 1). Like other terminal lakes, its size, depth, and salinity fluctuate in response to wet and dry periods in the region. Causeways were constructed beginning in the 1959 to accommodate rail and automobile traffic across the lake. These rock-fill causeways have divided the lake into four major portions, each with distinct salinity regimes. Farmington and Bear River Bays on the east side of the lake receive the majority of river inflows, and are essentially estuaries with salinities normally ranging from 0–90 g L^{-1}. A railway causeway divides the main lake into two main basins. In the southern section (Gilbert Bay) salinities normally range from 100 -180 g L^{-1}. Water then flows northward from Gilbert bay through passages in a railway causeway into Gunnison Bay where it evaporates to saturation (ca. 330 g L^{-1}).

The Great Salt Lake, like many other saline ecosystems, is environmentally and ecologically important for the birds that visit the lake and surrounding wetlands each year (Aldrich and Paul 2002). Due to the absence of fish from most of the lake, various birds are the main predators of brine shrimp, brine flies and other invertebrates inhabiting these saline systems. Additionally, harvest of brine shrimp cysts for aquaculture use is a multi-million dollar industry. Changes in the ecosystem that limit the population of aquatic invertebrates will affect these birds that visit the lake for feeding or breeding.

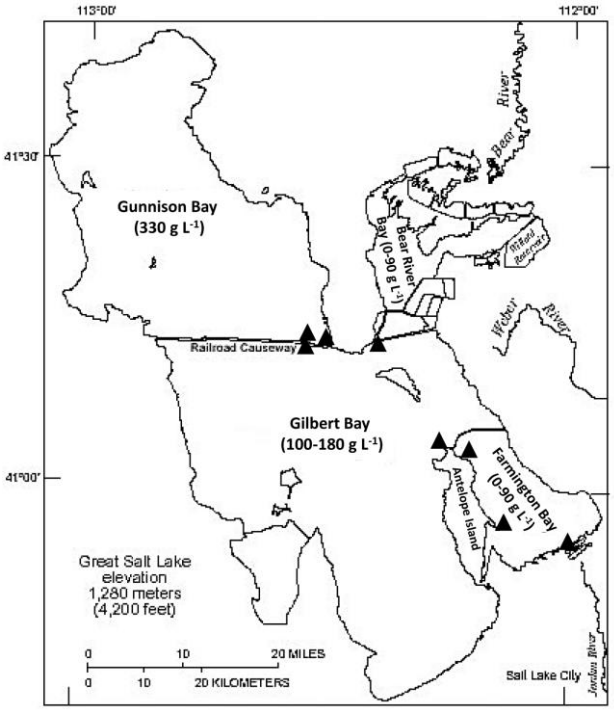

Figure 1. Map of the Great Salt Lake showing its four bays with common salinity ranges in each. Diamonds (▲) indicate areas where water, organisms and sediments were collected to seed the experimental microcosms.

We designed and conducted a microcosm experiment to study nearly the full range of salinities observed in the Great Salt Lake. The results will help saline lake managers understand how long-term water development in the basin and changes in runoff due to climate change will influence the salinities and consequently the production of invertebrates in the lake and serve as a case study for saline lake managers worldwide.

Methods

***Study Area and Organism Collection*—**The goal of the microcosm experiment was to isolate salinity as the only variable in a laboratory setting, while attempting to simulate the natural conditions in the Great Salt Lake as nearly as possible. The microcosms included water and plankton, sediment and macroorganisms from the Great Salt Lake collected from four sites (Fig. 1, Supplemental Table S1) in Farmington Bay, two in Gilbert Bay and two in Gunnison Bay with salinities ranging from nearly fresh

water (4 g L^{-1} salinity) to water near saturation (310 g L^{-1}). The goal of these collections was to provide living organisms, resting eggs and spores of zooplankton and algae as seed organisms for the microcosms.

Zooplankton for the microcosms were collected in October 2012 using a 250-µm net using horizontal tows in mid-Farmington Bay and just north of the marina on Antelope Island in Gilbert Bay. Brine fly larvae were collected in February 2013 when the lake temperature was -2°C using a hose and diaphragm pump attached to a bristle brush that dislodged the larvae from stromatolite surfaces. The Gilbert Bay samples consisted largely of *Artemia* and *Ephydra.* The Farmington Bay samples were from less saline water and included crustacean zooplankton including copepods, and cladocerans as well as predaceous *Trichocorixa verticalis* (water boatmen). Sediment was collected in October-November 2012 with a shovel at the Farmington Bay refuge canal, just east of Antelope Island in northern Farmington Bay, the southern Gunnison Bay sandy shore, and the northern Gilbert Bay shore. Water and organisms from each locale were stored with water from collection sites in aquaria in a well-lit room with a 12:12 light:dark cycle. The temperature in the room was slowly raised to the experimental level (25°C). Sediment was stored in buckets and periodically rehydrated until the start of the experiment.

***Microcosm design*—**The study was conducted in 15-L polyethylene buckets, with 12 L of water per microcosm. The microcosms were prepared at 12 nominal salinities starting at 10 g L^{-1} then ranging from 25 to 275 g L^{-1} at intervals of 25 g L^{-1}, with two replicates per treatment. While two replicates provided low statistical power to interpret specific differences between treatments using ANOVA and post-hoc tests, the finer salinity resolution facilitated analyses of large-scale trends in the responses utilizing regression analyses and graphical interpretation. Salinities were achieved using 11 L of deionized water, 1 L of mixed lake water (see below) and an inorganic salt mix using 84% Instant Ocean® Aquarium Sea Salt Mixture, 14% NaCl, and 3% K_2SO_4 by weight. This mixture yielded an ion concentration similar to that of the Gunnison Bay of the Great Salt Lake (Table 1). The 10 g L^{-1} nominal treatment was the minimum salinity possible with 1 L of mixed lake water and sediments that contained salts. Water in the

buckets was aerated and mixed through a glass tube extending to the bottom of each bucket and flow rates of 3-5 mL sec^{-1}. Buckets were covered with 1.6-mm mesh screen lids to prevent unwanted colonization and escape of emerging insects, and a 3 x 3 x 2 cm block of foam was added to give brine fly adults a resting place. To account for evaporation we gently added deionized water to the surface of each microcosm at one-week intervals to maintain constant 12-L volumes and salinities. These additions also provided a low-salinity overlying layer where brine shrimp cysts could hydrate and hatch. This was done to simulate freshwater inflows or rainfall events to the lake that allow hatching of *Artemia* cysts (Persoone and Sorgeloos 1980). Aeration was interrupted for 24 hours following the deionized water additions to prevent mixing. Buckets were placed on a light table and randomly repositioned on a weekly basis.

To provide an initial inoculum of phytoplankton and bacterioplankton for the microcosms we used 250 mL of lake water from each of four sources: Farmington Bay freshwater canal, Farmington Bay, Gilbert Bay, and Gunnison Bay (Fig. 1). This water was filtered through a 153-µm sieve to remove macroorganisms. The microcosms were then incubated in a controlled temperature room at 25°C with a photosynthetic active radiation intensity of 150 µmol m^{-2} s^{-1} with a 16:8 light:dark cycle. The temperature simulated the high summer conditions in the lake, and allowed community responses within the 30-day interval of the experiment. Nitrogen and phosphorous were added to each tank (100 µg $P \cdot L^{-1}$ as Na_2HPO_4; 700 µg $N \cdot L^{-1}$ as NH_4NO_3) to reach target concentrations similar to average lake nutrient conditions. Salinity was measured with a 0-28% range refractometer, but was converted to g L^{-1} units using the following equation of W. Gwynn (unpublished):

$$\text{Salinity (g L}^{-1}) = 0.082\ (\%\ \text{Salinity})^2 + 9.96\ (\%\ \text{Salinity}) - 0.44 \quad \text{(Equation 1)}$$

After three days of algal growth, sediment was added to each microcosm. This day will be referred to as Day 0 (15 March 2013). A homogenous mixture of moist sediment from each locale

Table 1. Ionic weight proportions of the Gunnison Bay (328 g L^{-1}) and Gilbert Bay (110 g L^{-1}) of the Great Salt Lake (from Sturm 1980) and measured ionic composition of water from six of the salinity treatments in the microcosm experiment.

	Great Salt Lake		Microcosm Experiment (Nominal Salinities)					
Major Ions	Gunnison (328 g L^{-1})	Gilbert (110 g L^{-1})	10 g L^{-1}	50 g L^{-1}	100 g L^{-1}	150 g L^{-1}	200 g L^{-1}	250 g L^{-1}
Na^{+}	.320	.313	.350	.330	.307	.314	.313	.320
K^{+}	.026	.027	.017	.025	.024	.025	.024	.025
Mg^{+2}	.032	.035	.037	.020	.017	.016	.016	.016
Ca^{+2}	.001	.002	.004	.001	.001	.001	.001	.001
Cl^{-}	.554	.551	.502	.538	.571	.562	.563	.562
SO_4^{-2}	.067	.073	.090	.086	.080	.082	.083	.076

Table 2. Nominal and mean (N = 2) measured salinities of the microcosm treatments over the course of the experiment. The salinities are given as either grams per liter, or as percent. Equation 1 was used to convert between the two types of units.

Nominal Salinity (g L^{-1})	Mean salinity (g L^{-1}) ± s.d.	Mean salinity (%)
10	9.6 ± 0.6	1.0
25	27.8 ± 0.1	2.8
50	51.2 ± 0.0	5.0
75	74.0 ± 0.6	7.1
100	99.5 ± 0.3	9.3
125	127.0 ± 0.5	11.7
150	150.4 ± 0.7	13.6
175	177.4 ± 0.4	15.8
200	196.0 ± 2.0	17.3
225	223.7 ± 1.7	19.4
250	250.0 ± 2.5	21.4
275	269.4 ± 1.6	22.8

described above was added by weight (500 g), providing approximately a 1-cm thick sediment layer in each bucket.

Zooplankton were added to each microcosm 1-2 hours following the sediment addition on Day 0. *Artemia franciscana* cysts from a Great Salt Lake source were hatched in 28 g L^{-1} NaCl. The resulting nauplii were added to each microcosm at a density of approximately 10 L^{-1}. Additionally, an equal mix of male and female adult *Artemia* were added to each bucket to provide a density of 1 L^{-1}. Copepods and cladocerans from the freshwater canal were also inoculated into the 0-100 g L^{-1} salinity treatments, but not in the higher salinities because the supply was limited and they were not expected to survive at the higher salinities. Because saturating nutrients were added at the start of the experiment, the addition of these organisms should not have influenced the abundance of any limiting nutrients. There was also a limited availability of *Trichocorixa verticalis* to inoculate the microcosms: however, two individuals were added to each bucket in the 0-125 g L^{-1} salinity treatments on Day 2 of the experiment. This yielded a density of 0.17 L^{-1}, well below peak densities of 1.3 L^{-1} that have been observed in Farmington Bay (Wurtsbaugh and Marcarelli 2006).

Benthic organisms were added on day 1 or 2. The second and third instar *Ephydra* (only *E. gracilis* were found in the initial samples) larvae that had been collected from Gilbert Bay were acclimatized by raising the temperature ca. 1.5°C day^{-1} over a 2-week period. They were then counted and added to the microcosms to provide initial densities of 195·m^{-2}. Chironomid larvae of the salt-tolerant genus *Cricotopus* (*Isocladius*) sp., from Farmington Bay were also added to reach an estimated density of 66 m^{-2}. One fish (*Gambusia affinis*) weighing 0.12-0.18 g was added to each of the 10-50 g L^{-1} salinity treatments to provide a biomass similar to that within mesotrophic lakes (~ 40 kg ha^{-1}). Fish were not included in higher salinity treatments because those salinities were far above the tolerance of the tested species. Within two hours, the fish in both the 25-50 g L^{-1} treatments had died and were removed to

prevent excess nutrient release, thus the lowest salinity treatment (10 g L^{-1}) was the only one that contained fish.

***Parameter measurements and organism sampling*—**Salinity and temperature were measured two times per week, once before each freshwater addition, and once after aeration was reestablished. Measured salinities varied little from our intended salinity targets (<5 g L^{-1}) and there was little variation between replicates (Table 2). The overall mean temperature of all treatments during the experiment was 24.9°C. However, temperatures varied somewhat with salinities: in the lowest salinities mean temperatures were 24.4°C whereas in the highest salinities they were 25.7°C. pH was measured three times during the experiment with an In Situ® Sonde: higher pHs were found in the 10-50 g L^{-1} salinity treatments (mean 9.0) compared to a mean pH of 8.2 at the three highest salinities. We also analyzed water from six treatments on the final day of the experiment to ensure the major ions we expected were present (Table 1). These water samples were frozen and cations were subsequently analyzed using ICP-mass spectrophotometric analyses, and chloride was analyzed using the mercuric thiocyanate method on a Lachat autoanalyzer.

Nutrient samples for total nitrogen (TN) and total phosphorus (TP) were collected from the middle of one replicate of each salinity treatment on days 0, 15 and 30 and stored in polyethylene bottles at -20°C until analyzed using persulfate digestion and the autoanalyzer method of Valderrama (1981). Phytoplankton chlorophyll *a* and phycocyanin levels were also measured from samples on days 0, 15, and 30. To measure chlorophyll *a*, 10-mL of water was filtered through 1-µm Gelman A/E filters and frozen. Chlorophyll *a* from the frozen filters was extracted in 10 ml of 95% ethanol for 20-24 h and analyzed with the non-acidification method of Welschmeyer (1994) on a Turner 10-AU fluorometer. Phycocyanin pigment, an indicator of cyanobacterial biomass, was analyzed in samples of raw water from each bucket with the Turner 10-AU fluorometer and Turner's phycocyanin optical kit that utilizes narrow-band interference filters with excitation and emission wavelengths of 630 and 660 ηm, respectively.

On Day 30 of the experiment, zooplankton and "benthic" organisms in the water column were sampled by pouring ca. 95% of the water from each bucket through an 80-µm sieve, preserved with 3-5% formalin, and subsequently counted and measured with an eyepiece micrometer at 10-30 X magnification with a dissecting microscope. The remaining benthic organisms and sediment were poured into 125 mL sample cups and preserved in 75% ethanol, elutriated to remove inorganic material, and then organisms contained therein were counted and measured. Using these procedures any dead organisms that had not decomposed would have been included in our estimates of densities and biomass. However, given the 30-day length of the experiment, most taxa that could not tolerate a given salinity would have begun decomposing before the end of the experiment. Several species of zooplankton were found in the benthic samples; however these were added to the pelagic calculations, as this was likely due to sampling technique. Similarly, we included any *Ephydra* found in the water column as part of the benthic community. Biomasses of each taxa were estimated by measuring lengths at 10-30X with a microscope, and converting these to mass using length-weight equations in Wurtsbaugh (1992) and Wurtsbaugh et al. (2011).

Periphyton was sampled on day 30 using a razor blade to remove material from a 4-cm wide and 24-cm high vertical section from the side of each bucket after the buckets had been drained and all other organisms were removed. Samples were frozen, extracted with 50 mL of 95% ethanol, diluted as necessary with ethanol, and periphyton chlorophyll *a* was measured with the Turner 10-AU fluorometer as described above.

***Statistical analyses*—**Because most parameters responded markedly to the different salinity treatments, and because variability was often high between replicates, we used $\log_{10}$ transformations to equalize variances. Most analyses were done as one-way analyses of variances followed by Fisher's Least Significant Difference (LSD) post-hoc tests using SYSTAT 8.0 (SYSTAT 1992). Linear regression analyses were done using Microsoft Excel 2010.

***Bioassay Experiment*—**Two sets of short-term 48-hour bioassays were done to test the tolerance of *Artemia* and brine fly larvae to different salinities. Two types of salts were used in these experiments. In 2012 we used a mixture of 50% NaCl and 50% Instant Ocean® inorganic salts that provides a composition relatively similar to that in Gilbert Bay (Table 2). In 2013 we utilized both this salt mixture and saturated brine from Gunnison Bay water that was diluted to provide appropriate salinities. Note that the Gunnison Bay water had a lower concentration of NaCl than the salt mixture of inorganic salts.

Artemia nauplii bioassays were done in 100 ml of water in 125 ml Erlenmeyer flasks held at a mean temperature of 25.5°C and 16:8 light-dark cycle. *Artemia* nauplii were hatched in the laboratory in 28 $g \cdot L^{-1}$ NaCl and temperatures of 28-31°C. In the 2012 bioassay, all nauplii were acclimated in a 15% salinity solution for 5 hours using the NaCl and Instant Ocean® salt mix. Then 10 to 16 nauplii were transferred from the hatching solution into the different NaCl + Instant Ocean salinity treatments. In 2013, the nauplii were first acclimated in 12% salinity Gilbert Bay water for 3 hours and then 20 nauplii were added to each flask. In the 2013 experiment we also tested gravid adult female *Artemia* and 2nd instar brine fly larvae. The *Artemia* and brine fly larvae were collected from Gilbert Bay at the northern tip of Antelope Island on 20 July, 2013 and held in the lake water at 140 $g \cdot L^{-1}$ (12.6%) salinity until the experiment was initiated on 22 July. They were then placed in 300 ml of test solution in 400-mL beakers. All flasks and beakers were covered with Parafilm® to minimize evaporation. Salinities and temperatures were monitored daily with a refractometer and digital thermometer, and after 48 hr. (± 1 hr.) the number of surviving individuals in each beaker or flask was counted using the naked eye. The nauplii were counted in a petri dish over a dark background to increase visibility. To determine if brine fly larvae were alive they were poked with a blunt rod to determine if they moved voluntarily.

Results

Densities of organisms—Final densities of juvenile plus adult *Artemia* in the microcosms were significantly influenced by salinity (1-way ANOVA, $p < 0.001$; Fig. 2A; Appendix I). No *Artemia* were found in the 10 g L^{-1} treatment where fish were present (see below). At salinities ranging from 25-100 g L^{-1} densities were very high (17-35 L^{-1}) and not statistically different (LSD; $p > 0.11$) at salinities ranging from 25-100 g L^{-1}. At 125 g L^{-1} *Artemia* densities decreased significantly to about 35% of those in the 25-100 g L^{-1} treatments. In salinity treatments greater than 150 g L^{-1}, densities of juvenile plus adult *Artemia* decreased to less than 3·L^{-1}, and they were nearly absent at salinities of 250 and 275 g L^{-1}. Of *Artemia* that did survive at higher salinities (above 150 g L^{-1}), almost all were adults, while lower salinities were comprised mostly of juvenile and nauplii stages (Fig. 2B). Nevertheless, in one of the 200 g L^{-1} treatments there were a moderate number of nauplii (3.8 L^{-1}), suggesting that some reproduction had occurred in quite high salinities. It is nevertheless possible, that these were nauplii from the inoculum that had survived to the end of the experiment.

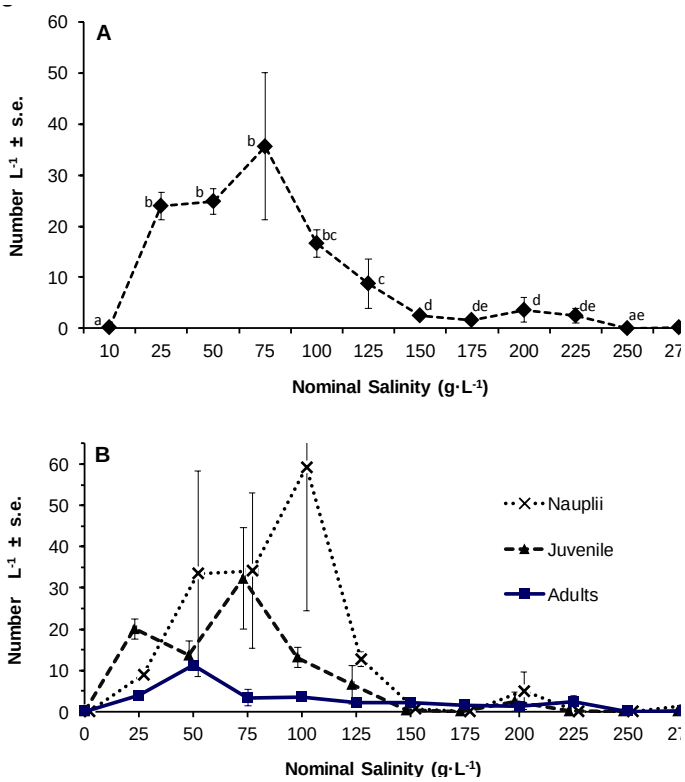

Figure 2A. Mean densities of juvenile plus adult *Artemia* in microcosms at 12 different salinities on day 30 (N = 2 per treatment). Symbols that share a common letter indicate treatments that were not significantly different (LSD, $p > 0.05$). B. Mean densities of three *Artemia* life stages on day 30 of the microcosm experiment.

A harpacticoid copepod (*Cletocamptus albuquerquensis*) was found in 50 g L^{-1} and lower treatments, most notably in the 25 g L^{-1} treatments, where there was a mean density of 780 L^{-1}. A small

rotifer (length – 0.1 mm), *Monostyla sp.*, was found in the 10 g L^{-1} salinity treatments at mean density of 1175 L^{-1}, but it was not found in any other salinity treatments. *Trichocorixa* occurred at densities of 0.1-density of 4.4 individuals^{-1}, consisting of mostly young juveniles (mean length 2.8 mm). This was the only replicate in which the *Trichocorixa* appeared to have reproduced, as the final density of corixids was greater than the initial. Samples from one 225 g L^{-1} microcosm contained two corixidae. This was likely due to contamination during sample processing, as *Trichocorixa* were not present in any other treatments exceeding 125 g L^{-1}, and 225 g L^{-1} is well beyond the known tolerance range for this genus.

Ephydra was the only benthic invertebrate remaining in the microcosms on the final day of the experiment (Appendix I). Some combination of larvae and pupae *Ephydra* were found in all but the 10 g L^{-1} salinity treatment where fish were present. Virtually all were *E. gracilis*, with one *E. hians* pupae found in a 75 g L^{-1} treatment. Our initial control sub-sample contained no *E. hians*, which are found at very low proportions compared to *E. gracilis* in the Great Salt Lake (Collins 1980a), so a survival differential between the two species could not be obtained. In salinities <200 g L^{-1} the brine fly larvae were observed primarily on the bottom sediments, but above 200 g L^{-1} many appeared to be unable to sink and were suspended in the water column. *Ephydra* adults were observed on the water surface during the experiment, generally 1-2 days after the fresh water was added, but no more than 4 adults emerged in a single microcosm, and none survived to the final day of the experiment. Several larval chironomids were observed in the 10-25 g L^{-1} treatments on days 1-3 of the experiment, but none were observed after day 4. *Gambusia* only survived in the 10 g L^{-1} treatment, with densities of 1 per microcosm.

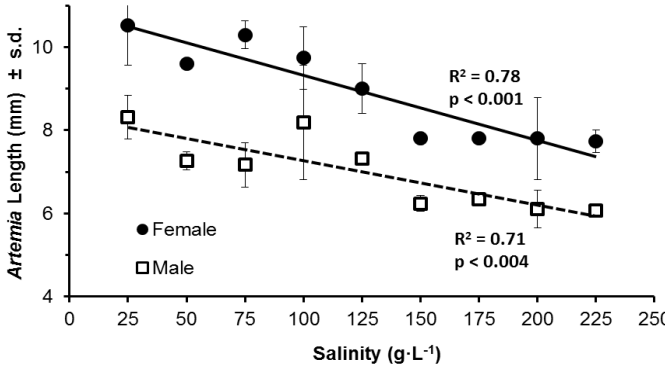

Figure 3. Mean lengths (n = 10) of adult male and female *Artemia* at 12 salinities on the final day of the microcosm study.

Species Lengths and Community Biomass— Just as salinity impacted *Artemia* densities, salinity exerted significant limitations on *Artemia* growth. Average adult *Artemia* lengths were reduced by approximately 30% (Fig. 3; Appendix II) from the lowest salinity in which they survived (25 g L^{-1}) to the highest salinity (225 g L^{-1}). The average initial female length was 7.9 mm, and this increased to 10.1 mm on day 30 in the 25-50 g L^{-1} treatments. In contrast final mean lengths were only 7.7 mm in the 150-225 g L^{-1} treatments. Similarly, the average inoculated adult male was 5.9 mm, which grew to a mean 7.8 mm in the 25-50 g L^{-1} treatments on Day 30, but only 5.5 mm in the 200-225 g L^{-1} treatments (Figure 3). The linear decrease in mean length with increasing salinities translated to nearly a three-fold decrease in the average estimated weight of an adult *Artemia*: In salinities of 25-50 g L^{-1} *Artemia* averaged 680 μg per individual, whereas at salinities from 200-225 g L^{-1} they averaged only 230 μg per individual. Similar to the effect on *Artemia*, increased salinities decreased the growth and final weights of *Ephydra* in the microcosms, but not their densities. The mean length of *Ephydra* larvae in the inoculum was 6.0 mm. Average final *Ephydra* larvae length was almost 40% less at higher than in the lower salinities (Fig. 4). Larvae in 25-75 g L^{-1} salinity treatments had a mean length of 7.5 mm while those in 200-250 g L^{-1} averaged 5.5 mm. There was no significant change in *Ephydra* pupae length. The shorter larval lengths resulted in a calculated decrease in the mean weight of individuals from approximately 1.1 mg to 0.6 mg over the salinity range.

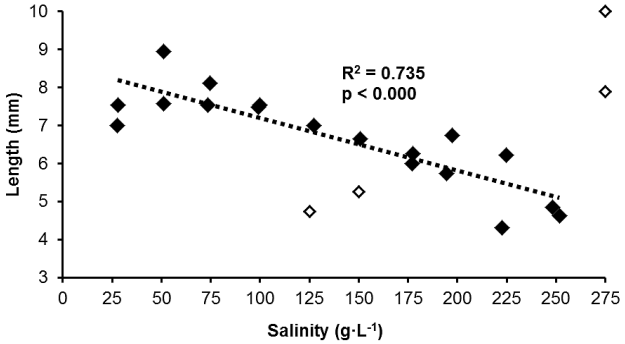

Figure 4. Mean lengths of *Ephydra* larvae (n = 10) in each replicate of the different salinity treatments on the final day of experiment. Microcosms with less than 4 individuals to sample (open symbols) were not included in the regression.

Microcosms at salinities greater than 50 g L^{-1} were subject to a decrease in zooplankton diversity and a decrease in biomass of all macroinvertebrates (Fig. 5A; Appendix II). Final zooplankton biomass was only 0.2 g L^{-1} (dry weight) in the 10 g L^{-1} treatment consisting of primarily rotifers with some

copepods (Fig. 5A). The fish in this low salinity treatment grew from initial wet weight of 0.12 g to an average 0.15 g wet weight and represented a mean biomass of 2.7 mg dry weight L^{-1}. In the 25 g L^{-1} treatment copepods represented over half of the pelagic biomass with a mean 3.4 mg·L^{-1}. *T. verticalis* had little to no impact on total pelagic biomass (Fig 5A). Mean total zooplankton biomass reached a maximum 6.7 mg·L^{-1} at 50 g·L^{-1} salinity, and then decreased rapidly never reaching more than 3 mg L^{-1} in salinities exceeding 50 g L^{-1} (Fig. 5A).

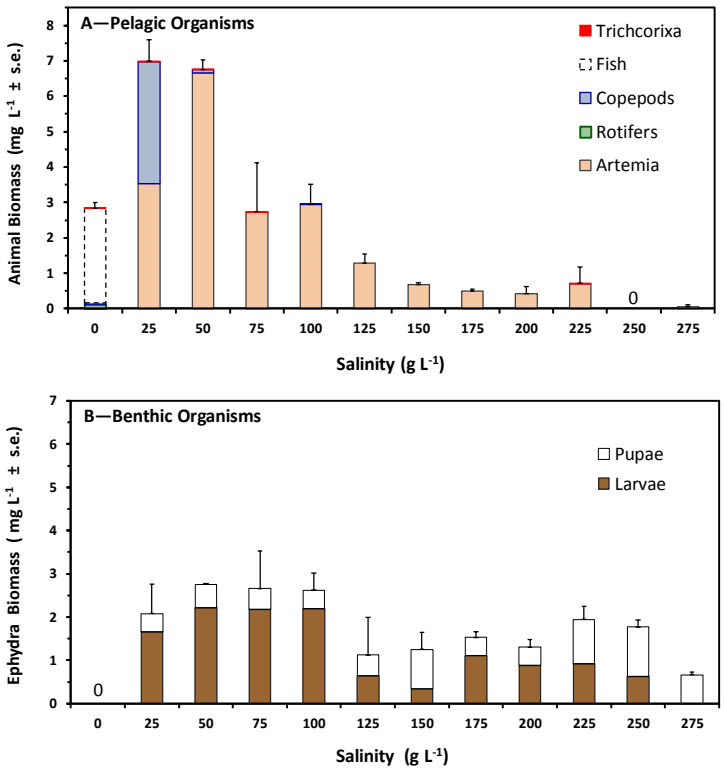

Figure 5. A. Biomasses of pelagic animals at the end of the 30-day microcosm experiment at 12 different salinities. B. Final biomasses of benthic invertebrates (brine flies) in the salinity treatments. Error bars show +1 s.e. of the total biomasses at each salinity.

Artemia dominated pelagic biomass in salinity treatments exceeding 25 g L^{-1} (Fig. 5A). Thus, pelagic biomass at salinities higher than this essentially mirrored *Artemia* biomass trends and values. Total *Artemia* biomass was greatest (6.7 mg L^{-1}) in the 50 g L–1 treatments due to dense population with large adults and juveniles in both replicates (Fig. 2A). The 25-100 g L^{-1} salinity treatments contained average *Artemia* biomasses greater than 2.0 mg·L^{-1} but variability between replicates was high in most treatments. *Artemia* biomass was less than 1.3 mg L^{-1} at salinities greater than 100 g L^{-1}, driven by both a drop in densities and in the mean weight of individuals.

Since *Ephydra* were the only benthic macroorganism found at the end of the experiment, their biomass was a direct indicator of total benthic invertebrate community biomass and structure (Fig. 5B). Consequently, benthic biomass was higher (2.1-2.8 mg L^{-1}) in the 25-100 g L^{-1} treatments, and significantly lower (LSD, $p < 0.05$) in salinities greater than 100 g L^{-1} (1.3-1.9 mg L^{-1}). At low salinities (10-75 g L^{-1}), pelagic organisms represented almost all the animal biomass. In intermediate salinities of 100-125 g L^{-1} the proportion between benthic and pelagic invertebrate biomass equalized at a 1:1 ratio. In excess of 150 g L^{-1}, benthic biomass represented the larger proportion of total community biomass, until greater than 90% of the total animal biomass was composed of brine flies in the 250-275 g L^{-1} salinity treatments. Thus, salinity appeared to change the balance of benthic and pelagic macroorganisms, although the degree to which this occurred was likely exaggerated due to the persistence of brine flies from the initial inoculation, as *Ephydra* may not be able to reproduce at the highest salinities we tested.

***Chlorophyll in Phytoplankton and Periphyton*—**Both time and salinity had significant effects on measured chlorophyll *a* levels in phytoplankton (2-way ANOVA, time, $p < 0.006$; salinity, $p < 0.002$). On Day 0 all treatments had concentrations of 7-14 μg L^{-1}. At the midpoint (Day 15), phytoplankton chlorophyll had decreased to less than 10 μg^{-1} in salinity treatments less than 200 $g\cdot^{-1}$ where more grazing zooplankton were present, while phytoplankton chlorophyll levels had risen to 27-49 μg L^{-1} in salinity treatments from 200-250 g L^{-1} (data not shown). On the final day of the experiment, the gap in measured phytoplankton chlorophyll *a* had widened between those treatments above and below 200 g L^{-1} (Fig. 6A; Appendix I). In the 10 g L^{-1} salinity treatment where *Artemia* were absent, mean chlorophyll levels were 11 $\mu g \cdot L^{-1}$ but in the 25 - 175 g L^{-1} treatments where they were abundant, mean chlorophyll concentrations were 2 μg L^{-1}. In salinity treatments at 200-275 g L^{-1} where *Artemia* abundances were low, the mean chlorophyll concentration was 128 μg L^{-1}. However, due to significant variability between replicates, statistically significant elevation of phytoplankton chlorophyll was only found in the 225-250 g L^{-1} salinity treatments (LSD, $P < 0.05$).

Cyanobacterial biomass, as measured by phycocyanin pigment concentrations, declined significantly (log regression; $p < 0.000$) with increasing salinity (data not shown). On the final day of the experiment, phycocyanin concentrations were highest in the 25 g L^{-1} treatment, and declined about 6-fold at a salinity of 125 g/L and remained low at higher salinities. However, phycocyanin concentrations were never high in any of the treatments with maximum relative Turner fluorescent units near 1. In contrast, relative units have reached 30 in Farmington Bay during blooms of the cyanobacteria *Nodularia* (Wurtsbaugh et al. 2012).

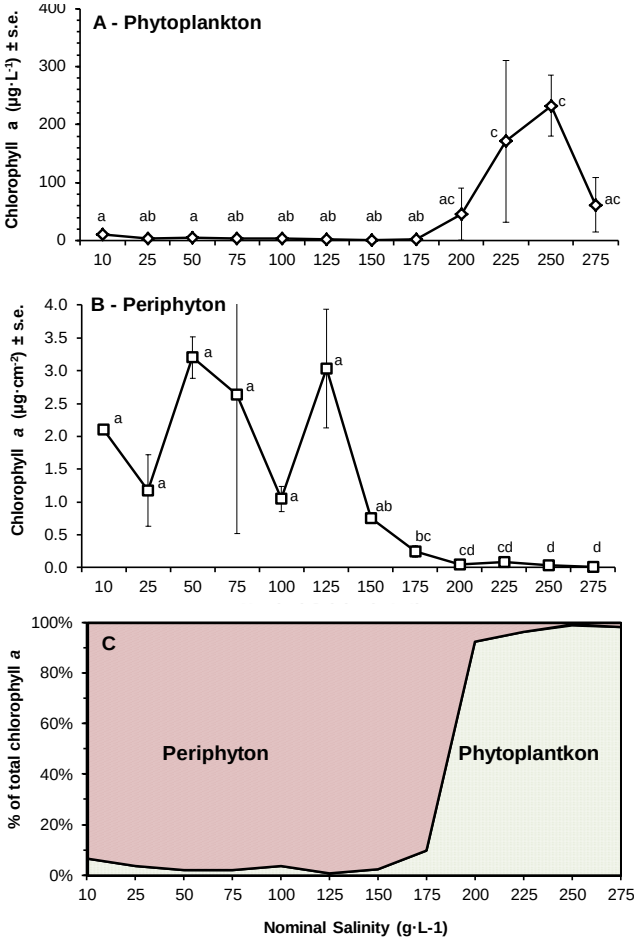

Figure 6A. Mean concentration of chlorophyll *a* in phytoplankton in 12 salinity treatment on the final day of the microcosm experiment (N=2). B. Mean concentration of chlorophyll *a* in periphyton taken from the sides of the buckets in the microcosm experiment. C. Relative distribution of total chlorophyll *a* total between periphyton and phytoplankton in each salinity treatment at the end of the 30-day experiment. Symbols that share a common letter indicate treatments that were not significantly different (LSD, $p > 0.05$).

Salinity also affected the distribution of algal biomass between phytoplankton (pelagic) and periphyton (benthic). Chlorophyll *a* concentrations in periphyton were elevated (1.1-3.2 µg·cm^{-2}) in salinity treatments < 150 g L^{-1} (Fig. 6B). In contrast, at salinities greater than 150 g L^{-1}, levels of periphyton chlorophyll did not exceed 1.0 µg·cm^{-2} (Fig. 6B) and were significantly lower (LSD, $p < 0.05$). When we calculated the proportions of total amount of chlorophyll in the microcosms, more than 90% was found in the periphyton at salinities less than 175 g L^{-1} (Fig. 6C). From 175 g L^{-1} to

225 g L^{-1} there was a rapid change in the proportion of chlorophyll in periphyton to phytoplankton: More than 90% of the chlorophyll *a* was found in phytoplankton at nominal salinities greater than 200 g L^{-1}.

Nutrients—At different salinities there were marked changes in the abundance of nitrogen, and consequently in the N:P ratios (Fig. 7). Total nitrogen levels in the water decreased with time, notably in the 10-125 g L^{-1} treatments, while at high salinities, nitrogen levels were more consistent as time progressed (Fig. 7A). These changes in TN were significant for both time and salinity level (2-way ANOVA without replication; time, $p < 0.000$; salinity, $p < 0.019$). Total phosphorous levels remained constant (0.6-0.9 mg·L^{-1}) through the experiment with little consistent variation between salinity treatments (Fig. 7B) and neither time ($p = 0.067$) nor salinity ($p = 0.133$) had significant effects on concentrations. At the beginning of the experiment, the N:P mass ratio in all treatments was >7.1:1 (Redfield ratio based on mass), potentially suggesting phosphorus-limited algal growth. However, because of the loss of nitrogen from the water column, the N:P ratio decreased markedly, particularly in salinity treatments below 150 g L^{-1} (Fig. 7C) where the ratio was < 4.0. The effects of both time and salinity on the TN:TP ratio were highly significant ($p < 0.000$).

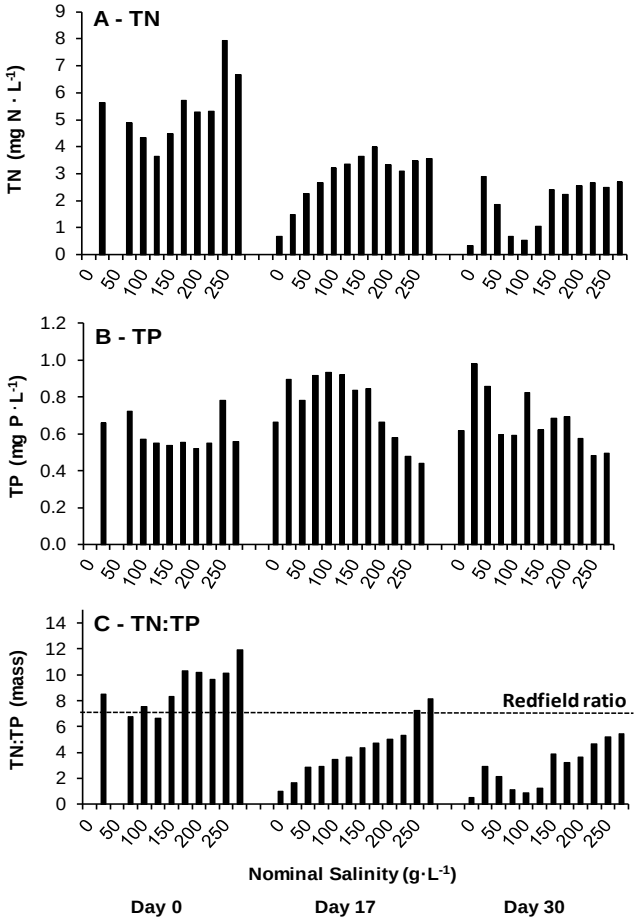

Figure 7. A. Concentrations of total nitrogen (TN); B. total phosphorus (TP), and; C. the TN:TP Redfield ratio (by mass) at 12 different salinities in the microcosms. Nutrients from only a single microcosm at each salinity treatment were analyzed. The dotted line in C shows the Redfield ratio of balanced nutrient levels for average phytoplankton.

Short-term (48 hr.) Bioassay Experiments— Survival of *Artemia* nauplii and gravid females decreased at higher salinities independent of salt mix or the year we performed the bioassays. In both years there was good agreement that above 230 $g \cdot L^{-1}$ (20%) salinity, nauplii survival was very low (Fig. 8A). At salinities from 100-200 $g \cdot L^{-1}$ nauplii survival was slightly better in the 2013 than in the 2012 experiment in both the inorganic salt mixture and Gunnison Bay salt treatments. Less data was available to evaluate adult female short-term survival (Fig. 8B), but it appeared that the threshold salinity causing high mortalities was somewhat higher (~250 $g \cdot L^{-1}$; 21.4%) than for nauplii. Short-term survival of brine fly larvae (Fig. 8C) was essentially 100% up to the highest salinity tested (322 $g \cdot L^{-1}$; 26.6%).

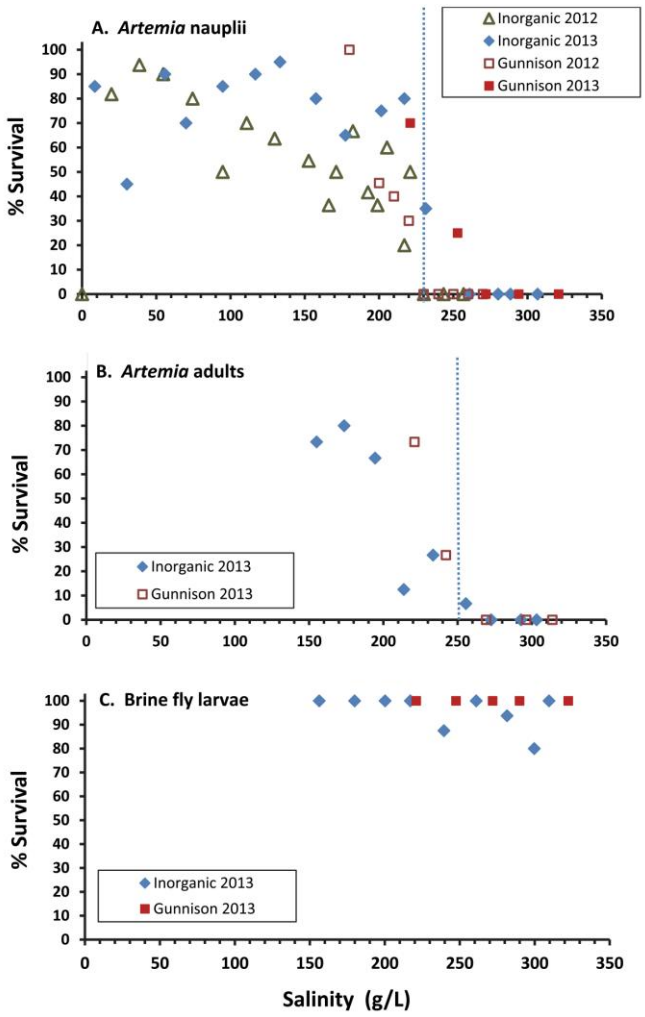

Figure 8. Percent survival of *Artemia* nauplii (A), gravid adult female Artemia (B), and brine fly larvae (C) after 48 hr. in different salinities. Two types of salt mixtures were used: (1) an inorganic salt mix of 50% NaCl and 50% Instant Ocean® salts, and; (2) saturated Gunnison Bay water from the Great Salt Lake that was diluted to the appropriate salinities. Vertical dotted lines indicate salinities were survival was normally <10%.

Discussion

Our results are informative on the comprehensive effects of salinity on individual species and aquatic food webs as a whole in the Great Salt Lake and others saline systems. We observed the effects of salinity on all parts of the community from primary producers to invertebrates and top predators. For example, salinities above 100 g L^{-1} essentially eliminated any predation on *Artemia* and *Ephydra*. While *Artemia* and *Ephydra* can grow at these higher salinities, our results suggest that these salinities limit growth and development of both species. The dramatic effects of salinity were also demonstrated in measures of algal biomass and nutrient concentrations.

Salinity stress—Although overall salinity is important, the actual ionic composition of the salts in solution is equally important (Herbst 2001). In natural, and especially laboratory settings, *Artemia* and other salt-adapted organisms are often limited in their osmoregulatory capacity by levels of certain ions within the brine solution (Bowen et al. 1985). Our salt mixture had an ionic composition such that organisms in our experiment should have exhibited better salinity tolerance than to pure NaCl solutions. *Artemia* can survive in the laboratory and in the Great Salt Lake at salinities as high as 300 g L^{-1} (Croghan 1958), but other laboratory studies have found that nauplii only tolerate 146-175 g L^{-1} of pure NaCl (Conte et al. 1973), which was only slightly lower than the tolerance of nauplii in our 48-hr LC_{50} bioassays which only tolerated 175-220 g L^{-1} of an Instant Ocean®/NaCl mix (93% NaCl), or 164-205 g L^{-1} NaCl. Ion analysis of water from our microcosms had ratios similar to those found in the Great Salt Lake and did not reveal any levels which would exceed the osmoregulatory capacity of brine shrimp for sulfate (greater than 29% molar anionic composition) or potassium (Na/K molar ratio less than 9) (Bowen et al. 1985), at least as measured by short-term bioassays. Note, however, that our analysis did not include carbonate levels (Table 1) that can also be toxic to organisms adapted to chloride-dominated waters (Bowen et al. 1985). An analysis of the toxicity of different ions to *Artemia* deserves more attention, because the ionic composition of the Great Salt Lake is changing, likely as the result of mineral extraction of sulfate and magnesium (W. Gwynn and W. Wurtsbaugh, unpublished data).

There are many factors that potentially contributed to the significant decrease in adult *Artemia* length, density and corresponding biomass at elevated salinities. The decrease in *Artemia* length with increasing salinities was similar to what has been found for a closely related species *Artemia monica* that occurs in Mono Lake, California (Dana and Lenz 1986). As salinities increased from 76-133 g L^{-1} in Mono Lake, there was an approximate 25% drop in adult *Artemia* length, similar to the approximate 30% decrease we observed in our microcosms. Our observed maximum *Artemia* length at 25 g L^{-1} was similar to the *Artemia* growth maximum found by Reeve (1963) at 35 g·L^{-1} salinity. We hypothesize several reasons for reduced *Artemia* growth and biomass at higher salinities. First, although *Artemia* are very effective osmoregulators, this regulation requires significantly higher energy inputs at higher salinities (Croghan 1958). High salinities also require early development of respiratory regulating capacity (El-Gamal 2011) through increased hemoglobin synthesis, further limiting available energy for normal growth and development. Additionally, oxygen availability decreases markedly when salinity increases, and this may reduce the respiratory capacity of invertebrates. For example, Sherwood et al. (1991) found that saturated oxygen concentrations in NaCl solutions decreased from 8.0 mg·L^{-1} to 1.7 mg·L^{-1} as salinity increased from 10 to 250 g L^{-1} (at 25°C). However, Vos et al. (1979) found that at constant low salinity (35 g L^{-1}) *Artemia* were able to adapt to oxygen concentrations as low as 2 mg·L^{-1} within several days of acclimation. While oxygen may play a role in limiting *Artemia* respiration and growth, *Artemia* have been known to survive at dissolved oxygen concentrations as low as 1 ppm (Persoone and Sorgeloos 1980) and even respiration studies have concluded that when food levels are adequate, the main limitation on *Artemia* growth with increased salinity is osmotic regulation (De Wachter and Vandenabbeele 1991). We also tested the hypothesis that high density and/or viscosity of high salinity water might reduce filtration rates of *Artemia*, and thus slow their growth. Slow-motion videos made with an Apple iPhone camera indicated, however, that beat frequencies of the filtering legs of adults were actually 20-30% higher at 150 g L^{-1} salinity than at 35 g L^{-1}.

Grazing and predation—To better understand the relationship between zooplankton grazing and phytoplankton abundance we estimated potential grazing rates of *Artemia* and copepods using length-filtration formulas found in Wurtsbaugh (1992), and an average clearance rate for rotifers (1.7 ml individual^{-1} day^{-1}; Bogdan and Gilbert 1982) of the size we observed in the microcosms. While these calculations only provide approximate estimates of actual filtration activity, at lower salinities zooplankton grazing (mainly by *Artemia*) appeared to limit phytoplankton abundance. This was particularly evident in the 25-100 g L^{-1} salinity treatments where estimated community filtration rates exceeded 100% filtration of the water column per day at the end of the experiment. Actual filtration rates, however, were possibly lower as maximum rates are calculated at very low phytoplankton abundance, and as phytoplankton availability increases, zooplankton reduce their grazing rate. For example, Reeve (1963) found that *Artemia* filtration rates dropped to only about 10% of their maximum rates when equivalent chlorophyll concentrations reached 10 μg L^{-1}. In salinity treatments of 125-175 g L^{-1} the estimated maximum grazing rates of 25-65% day^{-1} were apparently adequate to reduce phytoplankton abundances, although increased salinity stress on the algae may have also played a part. Brock (1975) found the optimum salinity for growth and photosynthesis in *Dunaliella* (presumably *D. salina*) to be 10-15% (107-167 g L^{-1}) salinity, with a 50% decrease in cell concentration at salinities greater than 200 g L^{-1}. Thus both salinity itself and grazing pressure likely limited algal growth in treatments greater than 150 g L^{-1}.

Just as zooplankton grazing limited algal biomass, predation likely reduced densities of *Artemia* and *Ephydra* in the low salinity treatments as others have observed (Hammer 1986, Williams 1998). In the 10 g L^{-1} treatments both of these species were absent, likely as the result of predation by the fish *Gambusia*. *Gambusia* did not survive in the 25 g L^{-1} treatment, but this is likely because we did not acclimate them to this salinity, because Chervinski (1983) reported that they can survive in salinities as high as 61 g L^{-1}. The abundance of *Artemia* in the 25 and 50 g L^{-1} treatments was not expected, as others have reported that invertebrate predators can control shrimp in that salinity range (Wurtsbaugh and Berry

1990, Williams 1998). Unfortunately, we were unable to stock the microcosms with normal summer densities (0.5 - 2/L; Wurtsbaugh and Marcarelli 2006) of the predator *Trichocorixa verticalis*, and the short duration of the experiment likely did not provide sufficient time for a complete numerical increase in this predator. The harpactocoid copepod, *C. albuquerquensis*, was very abundant ($780 \cdot L^{-1}$) in the 25 g L^{-1} treatment, and this species has been reported as a potential predator of *Artemia* (Hammer and Hurlbert 1990). However, even at very high densities, it was unable to substantially reduce *Artemia* densities, suggesting that it may not be an effective predator.

While predators in the low-salinity treatments likely reduced *Ephydra* densities, the highest salinities also limited *Ephydra* larvae growth and development. Our 30-day experiment and 48-hr LC_{50} bioassays support the conclusion that brine fly larvae can survive at salinities as high as 275 g L^{-1} for at least one month. Because brine flies are believed to grow from egg to pupae in 3-4 weeks and spend 2-3 weeks as pupae (Collins 1980b), our study was not able to assess the population cycle or reproductive capability of *Ephydra* at these salinities. The fact that *Ephydra* larvae were the same size, or even smaller, at the end of the experiment compared to those in the innocula suggests that significant stress was imposed by salinity on the larvae at salinities greater than 200 g L^{-1}. Herbst (2006) found a similar reduction in *Ephydra* size over a 90 to 200 g L^{-1} salinity range in salt ponds, which he speculated was due to osmoregulatory stress on the individuals. However, we also noted that at salinities greater than 200 g L^{-1}, the *Ephydra* were suspended in the water column, and thus would have had difficulty grazing on periphyton, for which their feeding structures are adapted (D. Herbst, personal communication). Additionally, we did not provide solid substrates nor acclimate the *Ephydra* to the different salinities, so they may have been unable to attach to the substrates available in the microcosms. We also found lower periphyton at the highest salinities, likely further reducing food intake and limiting growth of the *Ephydra*, consistent with another hypothesis of Herbst (2006) for brine fly growth limitation. Another indicator of stress was that at salinities > 200 g L^{-1} over 50% of the final *Ephydra* biomass was as pupae,

suggesting that despite low larval sizes, individuals were electing to curtail growth in the high salinity water.

In another study, Herbst and Blinn (1998) observed a continuous decrease in benthic algae as salinities rose from 50-150 g L^{-1}. Our results support their observations and suggest continued benthic algal growth repression beyond 150 g L^{-1}. Because periphyton distribution appeared to be uniform at all depths of the polyethylene bucket sides and the water column was shallow (0.3 m), we can assume that light was not a limiting factor in benthic algae growth. Though we did not analyze periphyton diversity, Herbst and Blinn (1998) observed a 50% reduction in benthic algal species at salinities greater than 75 g L^{-1} in their Mono Lake mesocosms.

Nutrient responses—Nutrient concentrations were altered markedly by salinity in the microcosms. The decreases in nitrogen concentration and the consequent changes in the TN:TP ratios in the microcosm experiments were two of the more distinct responses to the salinity treatments. Although total nitrogen concentrations decreased in all treatments, the decreases were greater at lower salinities. Epipelic nitrogen fixation rates are highest in lower salinity waters (Herbst 1998), so this response was not expected. The decreasing nitrogen concentrations were likely the result of denitrification in the microcosms, driven by anoxia in the sediments or possibly in the water column at night. Others have noted that increasing salinities decrease the amount of denitrification possible. For example, Shapovalova et al. (2008) found an almost continuous decrease in denitrification in hypersaline soda lakes as salinities increased from 0.2 to 4.4 molar Na, which would correspond approximately to salinities ranging from 12 to 270 g L^{-1} in our experiment. Similarly, Kulp et al. (2007) modified sediment slurries from two saline lakes and found that denitrification decreased markedly above salinities of 150-200 g L^{-1}, and Borin et al. (2013) found that both denitrification and anammox—two microbial nitrogen-removing processes—decreased at salinities > 95 g L^{-1} (9.2%), but were low at salinities greater than this in the chemocline of the Mediterranean Sea. In our experiment the greater loss of nitrogen in the lower salinity treatments

resulted in TN:TP ratios < 4 (by weight; 8.8:1 molar), suggestive of highly N-limited conditions for algal growth (Smith 1982). The lower N:P ratios at low salinities was somewhat unexpected, given that others have found that increasing sulfate concentrations in fresh and marine waters results in greater release of phosphorus from the sediments, thus decreasing TN:TP ratios (Blomqvist et al. 2004). The final TN:TP ratios in nearly all of the treatments were, however, below 7, and thus indicative of nitrogen limitation, and this is consistent with field and laboratory studies of nutrient limitation of algal growth in both the south and north arms of the Great Salt Lake (Stephens and Gillespie 1976, Post and Stube 1988, Wurtsbaugh 1988). Consequently, the decrease in phytoplankton abundance in the lower salinities by the end of the experiment may have been a consequence of this nitrogen limitation slowing their growth, and the high grazing rates of *Artemia* and other zooplankton. Ogata et al. (In Prep.) found that the combination of nitrogen limitation and high grazing pressure by *Artemia* substantially reduced phytoplankton abundance in a two-week nutrient addition bioassay.

Figure 8. The railway causeway across the Great Salt Lake has caused major changes in the salinities on the two sides. Bridge and culvert construction continues to modify those salinity levels. Photo by W. Wurtsbaugh

Conclusion

Salinity is only one of many environmental factors that may affect community structure in natural saline systems, but it is one of the most dynamic factors in terminal lakes such as the Great Salt Lake both due to anthropogenic and natural changes. Measures should be implemented to prevent and reduce changes that will artificially raise salinities further within the lake, as our results indicate that increasing salinities will decrease the production of brine shrimp and brine flies that birds rely on. Salinities also influence the production of *Artemia* cysts that are important for the aquaculture industry. Although, the *Artemia* production was maximal at salinities < 100 g L^{-1} in our experiment, the aquaculture industry at

the Great Salt Lake prefers salinities near 150 g L^{-1}, because relative levels of cyst production are higher than at lower salinities (D. Leonard, personal communication). Optimal salinities for producing *Artemia* for birds may consequently differ from those ideal for cyst production. Lake managers will need to consider future changes in complex issues including surface runoff, water withdrawals, diking, and climate change when making lake management decisions that influence salinities.

For example, the diking of the GSL has caused salinities in the North Arm to be in a range where *Artemia* and *Ephydra* populations are highly stressed, and consequently, where densities are very low (Post 1977; B. Marden and P. Brown, personal communication). Conversely, in the South Arm, salinity exerts fewer limitations on growth and development of *Artemia* and *Ephydra*. Overall salinities in the lake are also much higher due to water diversions for agriculture and urban use. Estimates of consumptive use indicate that the lake is 1.5-3.5 m (5-11 feet) lower than it would be if diversions had not occurred (Whitaker 1972, Klotz and Miller 2010). Because of the hypsographic shape of the basin, a 3.5 m decrease in elevation represents approximately a 50% decrease in the volume of the lake (Baskin 2005), and thus a doubling of salt concentrations. Additional planned diversions of water from the lake would further increase salinities and likely reduce the production of the important macroinvertebrates in the lake.

Acknowledgements

We want to thank Eric McCulley and Maureen Frank for assistance in collecting organisms for the study. The Central Davis Sewer District and Dave Barnes contributed airboat assistance to collect organisms. The comments of David Herbst and another anonymous reviewer substantially helped improve the manuscript. Javier Armengol provided information on filtration rates of rotifers and Matt Schroer identified the Chironomid larvae used in the experiment. The study was funded by the Utah Division of Forestry, Fire and State Lands, and by an undergraduate URCO research grant from Utah State University to B. Barnes. The Ecology Center at Utah State University and Environ Corporation helped administer the contracts.

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Appendix I. Salinities, chlorophyll concentrations, estimated filtration rates of the zooplankton, and densities of invertebrates in microcosms at the conclusion of the experiment.

Nominal Salinity (g/L)	Replicate	Actual Salinity (g/L)	Salinity (%)	Final Chlorophyll Concentration (ug/L)	Periphyton Concentration (ug/cm^2)	Community Filtration Rate (%/day)	Adult Artemia (#/L)	Artemia Juvenile (#/L)	Atermia Nauplii (#/L)	Ephydra Larvae (#/L)	Ephydra Pupae (#/L)	Tricorixia (#/L)	Harpacticoid Copepod (#/L)	Rotifers (#/L)
10	A	9.2	1.0	11.6	2.09	1%	0.1	0.1	0.0	0.00	0.00	0.00	0.0	67.5
10	B	10.0	1.0	10.4	2.11	43%	0.0	0.0	0.0	0.00	0.00	0.17	25.5	2283.0
25	A	27.9	2.8	3.6	1.72	295%	4.2	22.5	10.0	2.00	0.50	0.00	706.7	0.000
25	B	27.7	2.8	3.0	0.64	329%	3.7	17.7	8.0	1.42	0.08	4.42	851.7	0.000
50	A	51.2	5.0	6.7	3.52	334%	12.0	10.3	8.6	1.92	0.08	0.08	39.1	0.000
50	B	51.2	5.0	3.7	2.89	299%	10.3	17.1	58.3	1.75	0.67	0.08	0.0	0.000
75	A	74.4	7.1	3.0	4.75	64%	1.3	19.9	15.3	1.33	0.17	0.25	0.0	0.000
75	B	73.5	7.0	5.4	0.52	200%	5.4	44.6	52.9	2.75	0.50	0.00	0.0	0.000
100	A	99.7	9.3	3.1	1.24	117%	3.8	15.5	24.5	2.25	0.50	0.00	1.3	0.000
100	B	99.3	9.3	3.0	0.85	132%	3.3	10.7	94.0	2.08	0.08	0.00	0.0	0.000
125	A	126.6	11.6	1.9	2.13	50%	2.0	1.8	10.9	0.58	0.17	0.00	0.0	0.000
125	B	127.3	11.7	2.3	3.94	75%	2.3	11.3	14.6	1.42	0.50	0.00	0.0	0.000
150	A	150.9	13.7	1.7	0.79	38%	2.0	0.3	0.0	0.83	0.67	0.00	0.0	0.000
150	B	149.9	13.6	1.2	0.74	42%	2.2	0.4	1.4	0.17	0.58	0.00	0.0	0.000
175	A	177.6	15.8	2.1	0.34	27%	1.5	0.0	0.0	1.75	0.25	0.00	0.0	0.000
175	B	177.1	15.8	1.7	0.16	32%	1.7	0.0	0.0	1.33	0.33	0.00	0.0	0.000
200	A	194.6	17.2	90.2	0.04	33%	1.3	4.7	9.5	1.00	0.33	0.00	0.0	0.000
200	B	197.4	17.4	1.4	0.06	16%	1.1	0.2	0.4	1.33	0.25	0.00	0.0	0.000
225	A	222.5	19.3	31.6	0.15	69%	3.8	0.1	0.1	1.42	0.75	0.00	0.0	0.000
225	B	224.9	19.5	311.0	0.03	15%	0.9	0.1	0.0	1.75	0.67	0.17	0.0	0.000
250	A	248.3	21.3	285.0	0.05	0%	0.0	0.0	0.0	1.00	1.00	0.00	0.0	0.000
250	B	251.8	21.5	180.0	0.01	0%	0.0	0.0	0.0	1.75	0.58	0.00	0.0	0.000
275	A	268.6	22.8	14.4	0.01	5%	0.3	0.0	2.8	0.50	0.50	0.00	0.0	0.000
275	B	270.3	22.9	108.0	0.02	0%	0.0	0.1	0.2	0.42	0.42	0.00	0.0	0.000

Appendix II. Salinities, lengths and dry weight biomasses of invertebrates and fish in the microcosms at the end of the 30-day experiment.

Nominal Salinity (g/L)	Replicate	Artemia Male Mean length (mm)	Artemia Female Mean Length (mm)	Ephydra Larvae mean length (mm)	Fish Biomass (mg/L)	Total Artemia Biomass (mg/L)	Ephydra Pupae Biomass (mg/L)	Ephydra Larvae Biomass (mg/L)	Copepod Biomass (mg/L)	Trichorixia Biomass (mg/L)	Rotifer Biomass (mg/L)	Total Zooplankton Biomass (mg/L)	Total Benthic Invertebrate Biomass (mg/L)
10	A	-	-	-	2.57	0.00	0.00	0.00	0.00	0.000	0.006	0.01	0.00
10	B	-	-	-	2.75	0.00	0.00	0.00	0.11	0.002	0.219	0.33	0.00
25	A	7.9	9.8	7.5	0.00	3.24	0.72	2.04	3.12	0.000	0.000	6.36	2.76
25	B	8.7	11.2	7.0	0.00	3.78	0.12	1.28	3.77	0.034	0.000	7.58	1.40
50	A	7.1	9.6	9.0	0.00	6.82	0.12	2.63	0.17	0.002	0.000	7.00	2.75
50	B	7.4	9.6	7.6	0.00	6.33	0.97	1.81	0.00	0.000	0.000	6.33	2.77
75	A	7.5	10.5	8.1	0.00	1.29	0.24	1.54	0.00	0.006	0.000	1.30	1.79
75	B	6.8	10.1	7.5	0.00	3.99	0.72	2.80	0.00	0.000	0.000	3.99	3.53
100	A	7.2	9.2	7.5	0.00	2.32	0.72	2.29	0.01	0.000	0.000	2.33	3.02
100	B	9.2	10.3	7.5	0.00	3.27	0.12	2.10	0.00	0.000	0.000	3.27	2.22
125	A	7.4	8.6	4.7	0.00	0.99	0.24	0.00	0.00	0.000	0.000	0.99	0.24
125	B	7.3	9.4	7.0	0.00	1.51	0.72	1.28	0.00	0.000	0.000	1.51	2.00
150	A	6.1	7.8	6.6	0.00	0.63	0.97	0.69	0.00	0.000	0.000	0.63	1.65
150	B	6.4	7.8	5.3	0.00	0.72	0.84	0.00	0.00	0.000	0.000	0.72	0.84
175	A	6.3	7.7	6.3	0.00	0.45	0.36	1.30	0.00	0.000	0.000	0.45	1.66
175	B	6.4	7.9	6.0	0.00	0.55	0.48	0.92	0.00	0.000	0.000	0.55	1.40
200	A	6.4	8.5	5.7	0.00	0.59	0.48	0.64	0.00	0.000	0.000	0.59	1.12
200	B	5.8	7.1	6.7	0.00	0.23	0.36	1.12	0.00	0.000	0.000	0.23	1.49
225	A	5.9	7.9	4.3	0.00	1.17	1.09	0.56	0.00	0.000	0.000	1.17	1.64
225	B	6.2	7.5	6.2	0.00	0.24	0.97	1.28	0.00	0.000	0.000	0.24	2.25
250	A	-	-	7.5	0.00	0.00	1.45	0.48	0.00	0.000	0.000	0.00	1.93
250	B	-	-	4.6	0.00	0.00	0.84	0.77	0.00	0.000	0.000	0.00	1.62
275	A	-	7.9	7.9	0.00	0.10	0.72	0.00	0.00	0.000	0.000	0.10	0.72
275	B	-	-	10.0	0.00	0.00	0.60	0.00	0.00	0.000	0.000	0.00	0.60

Appendix III. Total N and total P concentrations on three days during the microcosm experiment. Only replicate A was measured in each salinity treatment.

Nominal Salinity (g/L)	Total N (mg/L)	Total P (mg/L)	TN:TP (by weight)
	Day 0		
0			
25	5.62	0.66	8.5
50			
75	4.88	0.72	6.8
100	4.33	0.57	7.6
125	3.66	0.55	6.6
150	4.47	0.54	8.3
175	5.74	0.56	10.3
200	5.30	0.52	10.2
225	5.33	0.55	9.7
250	7.94	0.78	10.1
275	6.67	0.56	11.9
	Day 17		
0	0.68	0.66	1.0
25	1.50	0.90	1.7
50	2.27	0.78	2.9
75	2.68	0.92	2.9
100	3.22	0.93	3.5
125	3.35	0.92	3.6
150	3.66	0.84	4.4
175	4.00	0.84	4.7
200	3.34	0.66	5.0
225	3.10	0.58	5.4
250	3.47	0.48	7.2
275	3.57	0.44	8.1
	Day 30		
0	0.32	0.62	0.5
25	2.90	0.98	3.0
50	1.86	0.86	2.2
75	0.68	0.60	1.1
100	0.54	0.59	0.9
125	1.05	0.83	1.3
150	2.40	0.62	3.9
175	2.22	0.68	3.3
200	2.54	0.70	3.7
225	2.67	0.58	4.6
250	2.51	0.48	5.2
275	2.70	0.50	5.4