

Salinity adaption and toxicity of harmful algal blooms in three bays of Great Salt Lake (USA)

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ABSTRACT

Cyanobacterial blooms can be harmful to animals and humans exposed to their toxins; however, their environmental drivers and boundaries still need to be elucidated. Salinity has been demonstrated to be an important driver of community composition that sets boundaries of species migration and survival. The filamentous cyanobacteria *Nodularia spumigena* forms dense blooms in estuaries around the world, produces the hepatotoxin nodularin, and has been thought to not survive or fix nitrogen (N) in high salinities. From 2005–2009 we studied three bays of Great Salt Lake (USA), two of which are estuaries with salinities ranging from 0 to >90 g l⁻¹ while the third, Gilbert Bay, had a salinity near 160 g l⁻¹. Bear River Bay and the larger Gilbert Bay were meso-eutrophic, while Farmington Bay, which receives direct inputs of secondary-treated sewage, was hypereutrophic with mean chlorophyll concentrations of 149 µg l⁻¹ and dense blooms of *N. spumigena*. Cell densities were >500 times those of *Nodularia* studied in the Baltic Sea. In Farmington Bay blooms occur at salinities ranging from 8–50 g l⁻¹, which are much higher than usually reported for this taxon. Concentrations of the cyanotoxin nodularin reached 660 µg l⁻¹ (mean = 41 µg l⁻¹), far above critical thresholds for contact recreation and above those causing bird mortalities elsewhere. The mean N₂ fixation rate of *Nodularia* measured over a salinity range of 14 to 52 g l⁻¹ was 47 mg N m⁻² d⁻¹, which is among the highest reported values for freshwater and marine ecosystems. The local adaptation of *Nodularia* to the extreme salinity conditions in Great Salt Lake furthers our understanding of salinity adaptation and the potential spread of this species to new regions.

1. Introduction

Eutrophication is a serious problem in inland waters, but it has frequently been dismissed as unimportant in saline lakes (e.g. Williams, 2002). However, terminal saline lakes accumulate pollutants, and consequently are often productive and therefore eutrophication can be a severe problem (Corrales-González et al., 2025; Tiffany et al., 2007a). Saline lakes frequently occur in arid regions remote from large cities, but due to their high productivity, and watery oases, they are extremely important for bird nesting and feeding (Herring et al., 2024; Tuite, 2000). Eutrophication from agricultural or urban sources can consequently threaten bird health and in some cases, that of humans (Carmichael and Li, 2006; Cowley et al., 2024; Hurlbert et al., 2007; Murphy et al., 2000).

Eutrophic aquatic ecosystems often host blooms of cyanobacteria. These have been extensively studied in freshwaters and estuaries (Wurtsbaugh et al., 2019), but less work has been done in saline lakes. Salinity levels can control which species survive in a given lake (Afionina and Tashlykova, 2024; Belovsky et al., 2025; Hammer, 1986), and together with global warming and eutrophication, influence species composition (Jeppesen et al., 2023). High salinities or the bioavailability of micronutrients in seawater and inland salt lakes may inhibit nitrogen (N₂) fixation by cyanobacteria (Howarth et al., 1988; Patiño et al., 2023), and thus the overall productivity of these systems because N is frequently the limiting factor for phytoplankton growth in saline systems (Pael, 2018; Wurtsbaugh et al., 2019). However, the details of salinity control on N₂ fixation are understudied.

We investigated the effects of eutrophication on cyanobacterial

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bloom formation and toxin concentrations in three bays of Great Salt Lake (USA), the largest saline lake in the western hemisphere. Two of the bays (Farmington and Bear River Bays) function as estuaries, with salinity gradients from their freshwater interfaces to their contact with the larger hypersaline Gilbert Bay (Fig. 1). Farmington Bay receives large inputs of secondary-treated wastewater from greater metropolitan Salt Lake City and has extensive blooms of the salt-tolerant cyanobacteria *Nodularia spumigena* (hereafter *Nodularia*). This species produces the hepatotoxin nodularin, which is similar in structure and potency as microcystins produced by the better-studied *Microcystis* sp. (Melaram et al., 2024; Rattner et al., 2022; Rinehart et al., 1988). Nodularins and microcystins may cause death in mammals and birds by liver hemorrhage, and both can also cause tumors at chronic low levels (Carmichael and Boyer, 2016; Yoshizawa et al., 1990).

Nodularia has been reported on all the continents, including Antarctica (Lehtimäki, 2000; Villalobos et al., 2025), but has been best studied in the brackish Baltic Sea where it coincides with populations of *Dolichospermum* sp. and *Aphanizomenon flos-aquae* (Munkes et al., 2021; Olofsson et al., 2020). Cyanobacteria blooms have commonly been noted in estuaries following heavy nutrient inputs (Bargu et al., 2011), but blooms are typically dominated by *Microcystis aeruginosa*. Curiously, *Nodularia* is rarely encountered in estuaries (Lehman et al., 2020; Moisander et al., 2002; Paerl, 1988) given its wide salt tolerance. We hypothesized that salinity would be a major factor controlling the transition between different cyanobacterial species in the bays and that high salinities would eliminate most of the filamentous cyanobacteria. We also hypothesized that all of the bays would be eutrophic because of heavy nutrient loading and the terminal nature of the lake which allows nutrients to accumulate.

2. Methods

2.1. Study area

Great Salt Lake (Fig. 1) is a 5200 km² system located in Utah, USA (41.04 N, 112.28 W). It is the largest saline lake in the Western Hemisphere with immense importance for migratory birds, recreation, and the harvest of minerals and brine shrimp (*Artemia*) eggs (Baxter and Butler, 2020; Wurtsbaugh and Sima, 2022). Because it is a terminal lake, its elevation and volume fluctuate with climatic cycles and water use in the watershed. During our study, the mean lake elevation was 1279.0 m (4196 ft.).

The lake has been divided by transportation causeways that separate it into four distinct bays that function somewhat independently (Table 1). The two bays on the eastern side of the lake receive freshwater

Table 1
Characteristics of the four bays of Great Salt Lake.

Bay	Characteristic			
	Area (Km ²)*	Mean depth (m)*	Salinity range (g l ⁻¹)	Deep Brine Layer
Farmington	170	0.78	8–99	Yes
Bear River	160	0.70	1–317	No
Gilbert	1770	5.00	60–172	Yes
Gunnison	1140	4.30	170–340	No

* Areas were derived from a 23 June 2006 MODIS satellite image and mean depths from (Root, 2023).

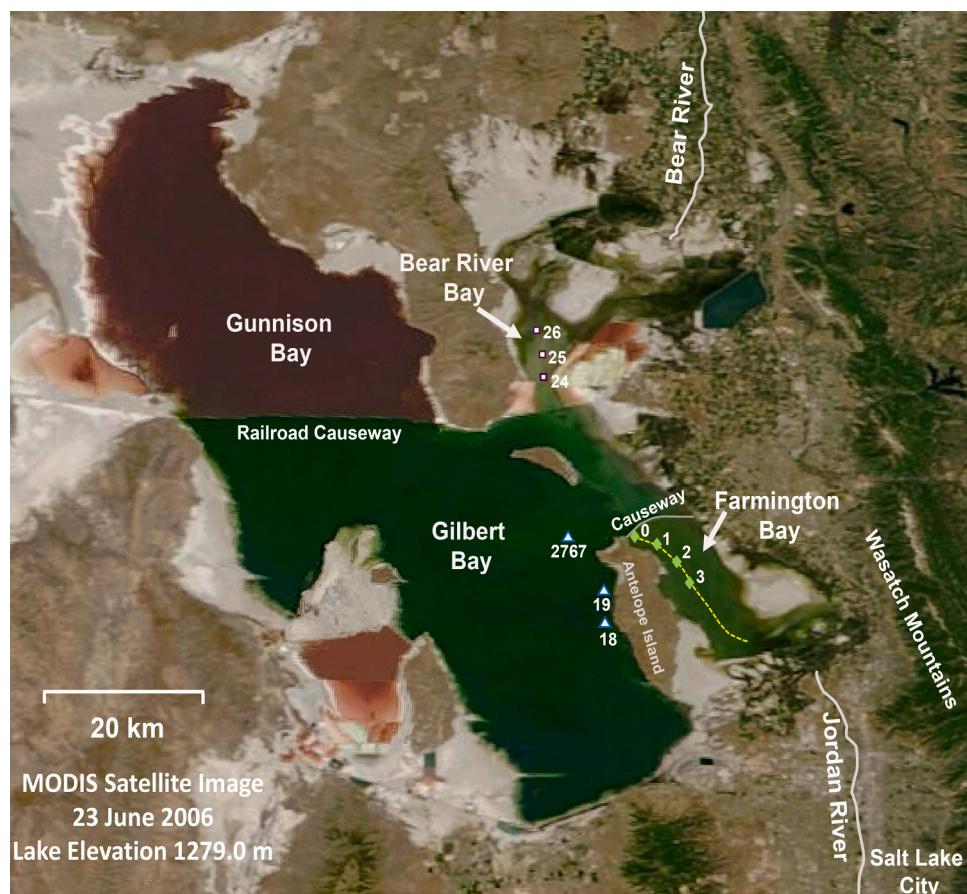


Fig. 1. Map of the Great Salt Lake showing the sampling stations used in the three bays in 2009. Identical or similar stations were sampled in other years. The yellow dashed line shows the sampling transect done in 2009. The lake perimeter shown is at an elevation 1279.0 m. During our study the lake elevation varied from 1279.2 m in 2007 to 1278.6 m in 2009. The red color of Gunnison Bay is due to the abundance of archaea (Baxter, 2018).

inflows from the mountains to the east and can be characterized as estuaries with salinities that vary from freshwater to hypersaline conditions, both spatially and seasonally. Farmington Bay and Bear River Bay were both shallow (<0.8 m), but depths and areas varied markedly between seasons and years. Farmington Bay receives inflow from the Jordan River, which passes through Salt Lake City and wetland areas before reaching the lake, from smaller creeks on the eastern side of the bay, and from three direct discharges from wastewater treatment plants (Fig. 1). During our study a salt wedge intruded from the saltier main lake (Gilbert Bay) so that the northern half of Farmington Bay was underlain with an anoxic, hydrogen-sulfide rich deep brine layer below a depth of ~1 m (Wurtsbaugh and Marcarelli 2004). Bear River Bay has fresh water during spring runoff since it receives inflows from the lake's largest tributary, the Bear River (Mohammed and Tarboton, 2012). Extensive submerged macrophytes and benthic filamentous algae communities covered much of the eastern portion of Bear River Bay where the water was fresh (Fig. 1). The main body of the Great Salt Lake was divided in two by the construction of a solid-fill railway causeway in 1959. A breach allows limited exchange of water and salts between these two bays. However, salinity in the northern Gunnison Bay is normally at NaCl saturation (~340 g l⁻¹). Consequently, Gunnison Bay was not sampled during the study because of its limited importance for birds and recreation in most years. Surface water salinities in the southern Gilbert Bay during our study varied from 145–180 g l⁻¹. However, approximately 50 % of Gilbert Bay was underlain by a deep brine layer due to density-driven return flows through the causeway from Gunnison Bay (Jones and Wurtsbaugh, 2014). This layer is anoxic and had high concentrations of toxic hydrogen sulfide and methyl mercury (Johnson et al., 2019).

Great Salt Lake has high nutrient loading due to agriculture in the basin and because 82 % of Utah's population of 3.5 million lives within the watershed. Secondary-treated wastewater from approximately 1.8 million people (2010 census; Wikipedia 2012) flow into Farmington Bay. Discharges of this wastewater are estimated to supply ~50 % of inflow to the bay (Meyers and Houston, 2006). Wastewater loading to Bear River Bay is less, with only 0.16 million residents in the watershed. Gilbert Bay receives wastewaters from 0.24 million residents in the Weber River basin and from the outflows of Farmington Bay and Bear River Bay (Naftz, 2017). A considerable portion of the flow from all three major rivers passes through wetlands before reaching the open waters of the lake, and consequently, some nutrients and other contaminants are removed and stored in these areas. Prior to 2009, all of the Great Salt Lake was managed with an Environmental Protection Agency (EPA) Class 5 designation which was protection for primary and secondary contact recreation, waterfowl, shore birds and other water-oriented wildlife. In 2009 the use classifications in Farmington and Bear River Bays were downgraded to only allow infrequent primary and secondary contact recreation.

2.2. Field sampling

Sampling was conducted in 2005–2007 and 2009 from the spring through fall at 3–4 sampling stations in each bay (Fig. 1). On each date, the northern, saltier, half of Farmington Bay was sampled where depths exceeded 0.5 m and could be accessed with a propeller-driven boat. In addition, in 2009 we sampled with an airboat along a longitudinal transect at 11 sites along the salinity gradient from the southern to northern end of Farmington Bay. In 2007, data recording sondes were placed at shallow sites (0.28 m deep) in Farmington Bay east of sites 1 and 2 to help describe the habitat utilized by shorebirds. Sites in Gilbert Bay were located 1–5 km off the west coast of Antelope Island. The shallowest sites in Gilbert Bay were in water 2–3 m deep, where microbiolites covered the bottom (Lindsay et al., 2020). The deeper site was near 7 m. Bear River Bay was only sampled in 2006 and 2009. Sampling sites there were located in the southwestern and saltier portion of the bay (Fig. 1).

Water transparency was measured with a 25-cm diameter Secchi disk with black and white quadrants. Salinity was measured with temperature-compensated refractometers with ranges of 0–10 % or 0–30 %. Refractometer readings in percent (x), were converted to gravimetric units (g l⁻¹) with equation 1:

$$y = 0.08165x^2 + 9.96334x + 0.43533 \quad r^2 = 0.999, n = 3145 \quad (1)$$

based on unpublished Great Salt Lake data from the Utah Division of Water Resources.

Troll 9500 multi-parameter sondes (In-Situ, Inc. Ft. Collins, CO) were used for continuous recording of temperature and water chemistry and real-time measurements of water column profiles. The sonde was equipped with an optical dissolved oxygen (DO) sensor.

Water samples for chemical and biological analyses were collected from the mixed layer with either an 8-cm diameter polyvinyl chloride (PVC) core sampler lowered into the mixed layer to a maximum depth of 1–1.5 m (2005, 2009), with a PVC horizontal Van Dorn bottle at a depth of 0.5 m (2005), or with a dip sample collected by immersing a polyethylene jug to a depth of 0.25 m (2006 and at all stations shallower than 0.3 m). A comparison of chlorophyll *a* (hereafter "chlorophyll") concentrations from samples collected at 0.5 m and with the integrated tube sampler in 2005 indicated that plankton were usually homogeneously distributed ($\text{Log Chl}_{0.5\text{ m}} = 1.034 \text{ Log Chl}_{\text{int}}^{0.999}; n = 62; r^2 = 0.99$). This suggests that the different collection methods from the mixed layer had little influence on parameter estimates.

2.3. Analytical methods

2.3.1. Nutrients and chlorophyll

Unfiltered water samples were frozen and analyzed for total nitrogen (TN) and total phosphorus (TP) after persulfate digestion (Valderrama, 1981). When salinities were higher than seawater, they were diluted to 35 g l⁻¹ prior to analysis. Following digestion, the samples were analyzed for nitrate (cadmium reduction) and phosphate (ascorbic acid molybdenum reaction) using an Astoria autoanalyzer (Astoria Pacific International, Portland OR). The detection limits for TN and TP were 6.0 and 3.0 µg l⁻¹.

Chlorophyll was measured as a proxy for total algal biomass by filtering 10 or 20-ml aliquots on 25-mm Gelman A/E filters with a nominal pore size of 1 µm. Two replicate samples were filtered from each station and kept frozen until analysis. Within three weeks, the filters were extracted in 95 % ethanol overnight, and the chlorophyll concentrations were measured with a Turner Designs 10AU fluorometer (Turner Designs, Sunnyvale, CA) using the Welschmeyer non-acidification technique and filter set (P/N 10-040R) (Welschmeyer, 1994). Phycocyanin pigment, an indicator of cyanobacterial biomass, was analyzed with the 10AU fluorometer and Turner Designs phycocyanin optical kit (P/N 10-305) that utilizes narrow-band interference filters with excitation and emission wavelengths of 600 nm and 640 nm, respectively. Three technical replicates were recorded for each sample.

2.3.2. Phytoplankton analyses

Phytoplankton densities and biovolume were analyzed from the 2009 samples by PhycoTech, Inc. (St. Joseph, MI) after filtration onto 0.45 µm membrane filters and mounting in methacrylic resin which clears the filter (Crumpton, 1987). One sample was counted from each station at magnifications varying from 400–1000X, depending on taxonomic composition. Measurements taken for biovolume calculations included the greatest axial linear dimension, and when necessary, additional measurements of width and depth. Cell and colony shapes were approximated to a geometric figure, and the appropriate calculation of biovolume was made following Hillebrand et al. (1999). For filamentous cyanobacteria, both vegetative cells and heterocytes were counted.

2.3.3. N_2 fixation

N_2 fixation was measured from May–November in 2005 at the northern station in Farmington Bay (Sta. 1). Water samples were collected at 0.2-m intervals from the entire mixed layer using a peristaltic pump. Samples were incubated in situ for ≥ 2 hr at 4–7 depths in 62-mL glass serum vials and fixation was measured with the acetylene reduction technique; methods and environmental conditions during incubations are detailed in Wurtsbaugh and Marcarelli (2006). Concentrations of ethylene in the samples were compared to the known concentrations in the standards and then converted to the amount of N_2 fixed using an assumed 3:1 ethylene: N_2 conversion ratio (Capone, 1993). To convert to daily rates, we assumed a 10-hr period of fixation.

2.3.4. Cyanotoxin analyses

Plankton samples for cyanotoxin analysis were filtered on GF/C glass fiber filters with 1- μ m pore size until the filter clogged. The filters were frozen at -70°C until shipped for analysis to SUNY College of Environmental Science and Forestry (NY). There the filters were extracted with 10 ml of acidified 50 % methanol using sonication (Boyer, 2007). These extracts were then assayed for cyanotoxins using three techniques: 1) the protein phosphatase inhibition assay (PPIA) via the method of Carmichael and An (1999) for microcystin and nodularin activity; 2) HPLC-MS for microcystin and nodularin variant identification (Boyer, 2020), and; 3) HPLC-MS for anatoxin-a and cylindrospermopsin identification following Boyer (2007). Method detection limits varied depending on the volume of water collected but were generally $< 0.5 \mu\text{g l}^{-1}$ for microcysts and $< 0.1 \mu\text{g l}^{-1}$ for anatoxin-a and cylindrospermopsin. Values for filtered samples represent only particulate toxin concentrations and were expressed in micrograms of toxin per liter of lake water. The PPIA analysis simultaneously detects the biological activity of all microcystin and nodularin variants. The HPLC analysis indicated that nodularin-R was the overwhelming dominant cyanotoxin in our analyses. Nevertheless, following standard protocols (Chorus and Bartram, 1999), we have expressed our results as the much more common microcystin-LR equivalents. We also analyzed for the neurotoxin anatoxin-a and the hepatotoxin cylindrospermopsin using HPLC-MS. These toxins were not detected in the samples, but anatoxin-a has been found previously in Farmington Bay zooplankton and benthic periphyton (Wurtsbaugh, 2011). Statistical analyses were performed using R (R Core Team, 2021) or Microsoft Excel.

3. Results

3.1. Physical-chemical characteristics of the three bays

Salinities in the three bays varied seasonally and annually, especially in the shallow Farmington and Bear River Bays (Fig. 2A). In the northern area of Farmington Bay salinities varied from 15–40 g l⁻¹ during spring runoff but climbed to 50–95 g l⁻¹ during fall as inflows subsided. Salinities in Bear River Bay were generally less but increased to over 250 g l⁻¹ when flows out of the bay ceased and evaporation concentrated the salts. In Gilbert Bay salinities varied from 140 to 170 g l⁻¹. Both Farmington and Gilbert Bays had salinity stratification beginning at 1 m and 6 m, respectively. The deep brine layers were anoxic and contained high concentrations of hydrogen sulfide (data not shown; Wurtsbaugh and Marcarelli, 2006).

Daytime surface (0.5 m) temperatures in the bays varied seasonally from near 0 °C in winter, to 24–28 °C in summer (Fig. S1). During winter when we did not sample, ice formed over the less-saline Farmington and Bear River Bays. The deeper Gilbert Bay usually had lower mid-day temperatures than shallow Farmington and Bear River Bays. Sonde data indicates minimal diel temperature variation in Gilbert Bay (Brothers et al., 2023), but in Farmington and Bear River Bays summer temperatures frequently varied 8–10 °C over the diel cycle, sometimes reaching 35 °C in shallow areas (Fig. S2).

Diel oxygen concentrations in the shallow Farmington and Bear

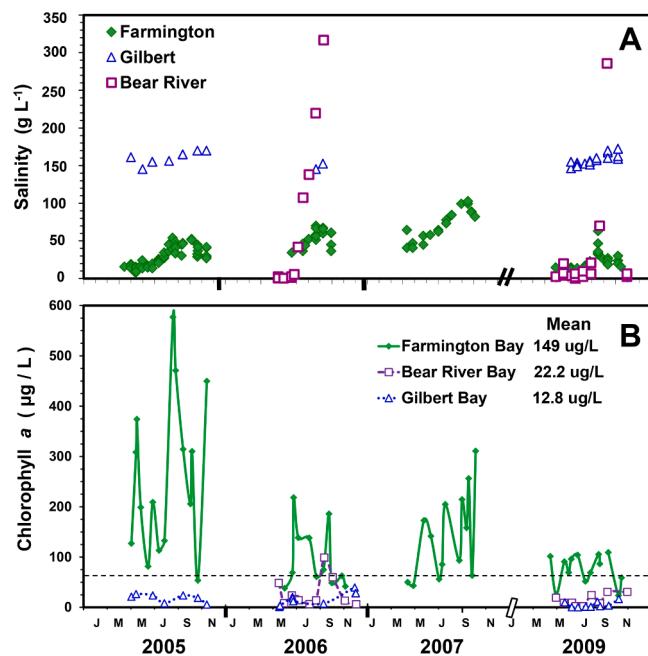


Fig. 2. A) Annual and seasonal trends in the surface water (0.2–1 m) salinity of Farmington, Gilbert and Bear River Bays of the Great Salt Lake in four years. Salinities shown here are only for areas of Farmington and Bear River Bays that were distant from river inflows. B) Chlorophyll *a* levels of phytoplankton in three bays of the Great Salt Lake, spanning the years 2005–2009. Most points show the mean of 2–4 stations. Note that little sampling was done in the winter months, when chlorophyll concentrations in Gilbert Bay often climb above 50 $\mu\text{g l}^{-1}$ because brine shrimp grazing ceases during this period (Wurtsbaugh and Gliwicz 2001, Belovsky et al. 2011). The dotted line shows the minimum level for hypereutrophic classification (Carlson and Simpson 1996). One-way ANOVA indicated highly significant differences in Chl. *a* between bays ($p < 0.001$) during comparable years (2006, 2009). A post-hoc Tukey test indicated that all bays were significantly different from each other ($p < 0.005$).

River Bays fluctuated significantly while fluctuations in Gilbert Bay were modest (Wurtsbaugh et al., 2002). In Farmington Bay summer oxygen concentrations frequently reached 25–35 mg l⁻¹ during the afternoon, and were often anoxic at night (Fig. S2).

Secchi depth transparencies in Farmington Bay were usually 0.2–0.4 m and somewhat higher in Bear River Bay (Fig. 3). Secchi depths in Gilbert Bay varied seasonally, from a low of 0.4 m in the late fall and winter, to over 4 m in summer when high rates of grazing from *Artemia* decreased phytoplankton to low levels (Belovsky, 2011; Wurtsbaugh, 1992).

Concentrations of TN and TP were high in all three bays, but particularly in Farmington Bay (Fig. S3). Over the three years that data was collected, respective geometric mean TP and TN concentrations in

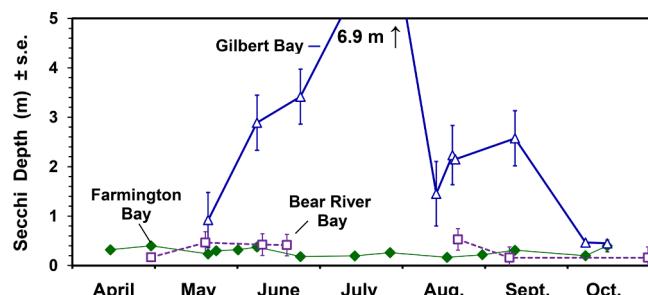


Fig. 3. Secchi depths in Farmington, Bear River and Gilbert bays in 2009. Error bars are for multiple stations. All the Secchi depth error bars for Farmington Bay lie within the symbol size.

Farmington Bay were 0.40 and 5.0 mg l⁻¹. In Farmington Bay, there was a general trend for TP to rise in summer, but in 2009 this trend was not obvious. In Bear River Bay, respective concentrations of TP and TN averaged 0.21 and 2.0 mg l⁻¹. However, these high values were due primarily to the dramatic increases in concentrations that were observed during mid-summer as the bay was drying. At other times of the year, nutrient concentrations were considerably lower in Bear River Bay than in Farmington Bay. For example, in 2009, total nutrient concentrations from spring through mid-July were 300–350 % higher in Farmington Bay than in Bear River Bay. In Gilbert Bay, mean TP and TN concentrations were 0.32 and 4.7 mg l⁻¹, respectively. These remained relatively stable over the sampling period. Mean molar TN:TP ratios were near 25:1 in Farmington and Bear River Bays, and 32:1 in Gilbert Bay.

3.2. Phytoplankton community, cyanotoxins, and N₂ fixation

Chlorophyll *a* levels from the spring through fall were extremely high in Farmington Bay, averaging 149 µg l⁻¹, but reaching over 300 µg l⁻¹ on several occasions (Fig. 2B). Chlorophyll levels in Bear River Bay were much lower, averaging 22 µg l⁻¹. Similarly, summer levels in Gilbert Bay were lower, averaging 13 µg l⁻¹, but they climbed to >40 µg l⁻¹ in the fall and winter when *Artemia* grazing ceased (Wurtsbaugh, 1992; Wurtsbaugh and Gliwicz, 2001). In Farmington and Bear River Bays chlorophyll concentrations were significantly correlated with phosphorus concentrations and consistent with this pattern for lakes in the U.S. National Lakes Assessment (U.S. Environmental Protection Agency, 2017; Fig. S4). Many Farmington Bay chlorophyll concentrations exceeded those in the Lakes Assessment. Studies in the Baltic Sea have shown that *Nodularia* benefits from phosphorus inputs and that the increased bloom is associated with an increase in overall toxicity (Schoffelen et al., 2018). Chlorophyll levels in Gilbert Bay, however, were not correlated with phosphorus levels, likely as a consequence of phytoplankton in this bay being N-limited (Stephens and Gillespie, 1976; Wurtsbaugh, 1988), and strongly controlled during the summer by top-down grazing pressure from *Artemia* (Wurtsbaugh, 1992).

Cyanobacteria dominated the plankton community in the northern part of Farmington Bay (Fig. 4A). From May–October *Nodularia* represented 80 % of the phytoplankton biovolume, followed by *Aphanothecace* sp. (4 %). Biovolumes of *Nodularia* reached over 200 mm³ l⁻¹ (Fig. 4A). *Nodularia* in Farmington Bay were abundant at salinities from 8 to 50 g l⁻¹ (Fig. 5), with densities well above the criteria for high health risk of 100,000 cells mL⁻¹ (World Health Organization, 2003). Surface blooms of *Nodularia* were present on some dates (Graphical Abstract; Wurtsbaugh et al., 2012). *Dolichospermum* sp. represented <0.01 % of the biovolume and *Aphanizomenon flos-aquae* was absent. In Bear River Bay (Fig. 4B) community composition was dominated by diatoms and chlorophytes. In Gilbert Bay chlorophytes (primarily *Dunaliella viridis*) and chrysophytes were dominant, although some cyanobacteria were found on one date (Fig. 4C). Total algal biovolumes in Bear River and Gilbert Bays were <10 mm³ l⁻¹.

Cyanobacterial toxins — Cyanotoxin concentrations were extremely high in the northern area of Farmington Bay, with nodularin concentrations averaging 41 µg l⁻¹, but reaching 663 µg l⁻¹ (Fig. 6). Toxin concentrations there were particularly high in 2009 when salinities ranged from 20–50 g l⁻¹ (Fig. 2A). Toxins were predominately nodularin-R with only minor amounts (<10 %) of a dimethyl Nod (Asp¹ or dhb⁵) present in a small number of samples. In a limited number of cases where we had both nodularin and cell counts, we found a mean cell quota 296 fg cell⁻¹ (Fig. S5; range 124–461; N = 17), among the highest levels reported in the literature (Pattanaik et al., 2010; Repka et al., 2001; Villalobos et al., 2025). There wasn't a significant relationship between salinity and cell quota ($p = 0.80$), although the sample size was low. Mean nodularin concentrations in Bear River and Gilbert Bays were only 0.3 and 0.5 µg l⁻¹, respectively. Microcystins (11 congeners), Anatoxin-a and cylindrospermopsin were not detected in any of the samples.

In August 2009 when *Nodularia* abundance was high, we sampled

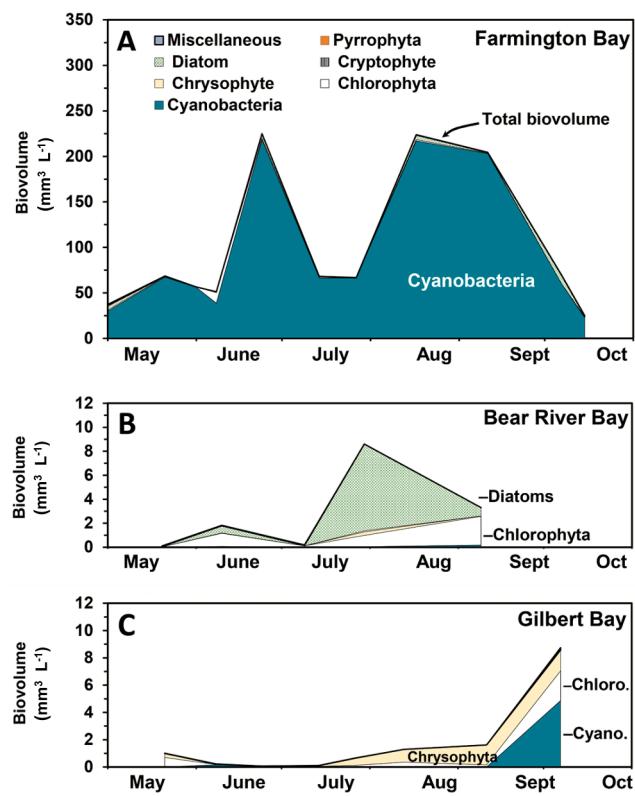


Fig. 4. Phytoplankton biovolumes in Farmington (A; Sta. 0, 1, 2, 3), Bear River (B; Sta. 24) and Gilbert Bays (C; Sta. 18 and 2767) of the Great Salt Lake during 2009. The top line of these stacked polygon graphs shows the total biovolume. Note that the scale for Farmington Bay is 35X greater than for the other bays. When averaged over the entire sampling period and all stations, *Nodularia spumigena* represented 91 % of the total cyanobacteria, and 86 % of total algal biovolume in Farmington Bay.

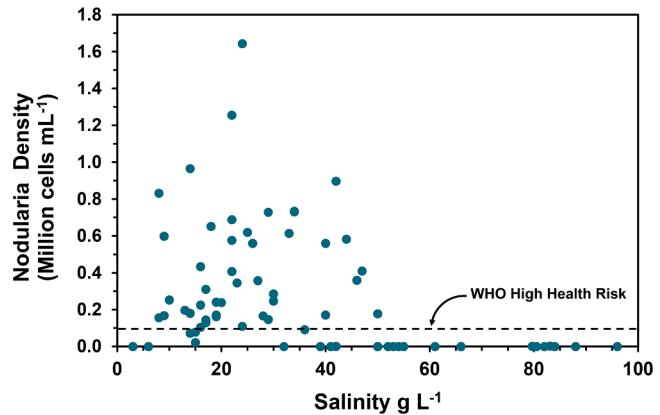
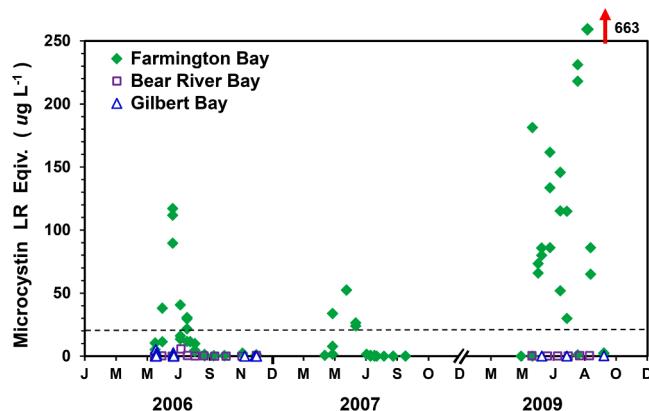


Fig. 5. Relationship between salinity and *Nodularia* cell densities in Farmington Bay. The dashed line shows the World Health Organization's (2003) criteria for a high probability of acute health effects of cyanobacteria.

along a salinity gradient in Farmington Bay from the north near the convergence with Gilbert Bay to the southern end near the inflow of fresh water. Single measurements of each parameter were done at each station, limiting the inferences we could make. At the northern end of the bay, salinities ranged from 33 to 63 g l⁻¹ but decreased to 3 g l⁻¹ near the river and wastewater inflows (Fig. 7A). Chlorophyll concentrations were 80–100 µg l⁻¹ at the northern end but peaked 16 km south where salinities were lower. Phycocyanin concentrations, as a proxy for cyanobacterial abundance, were highest in the northern part of the bay and



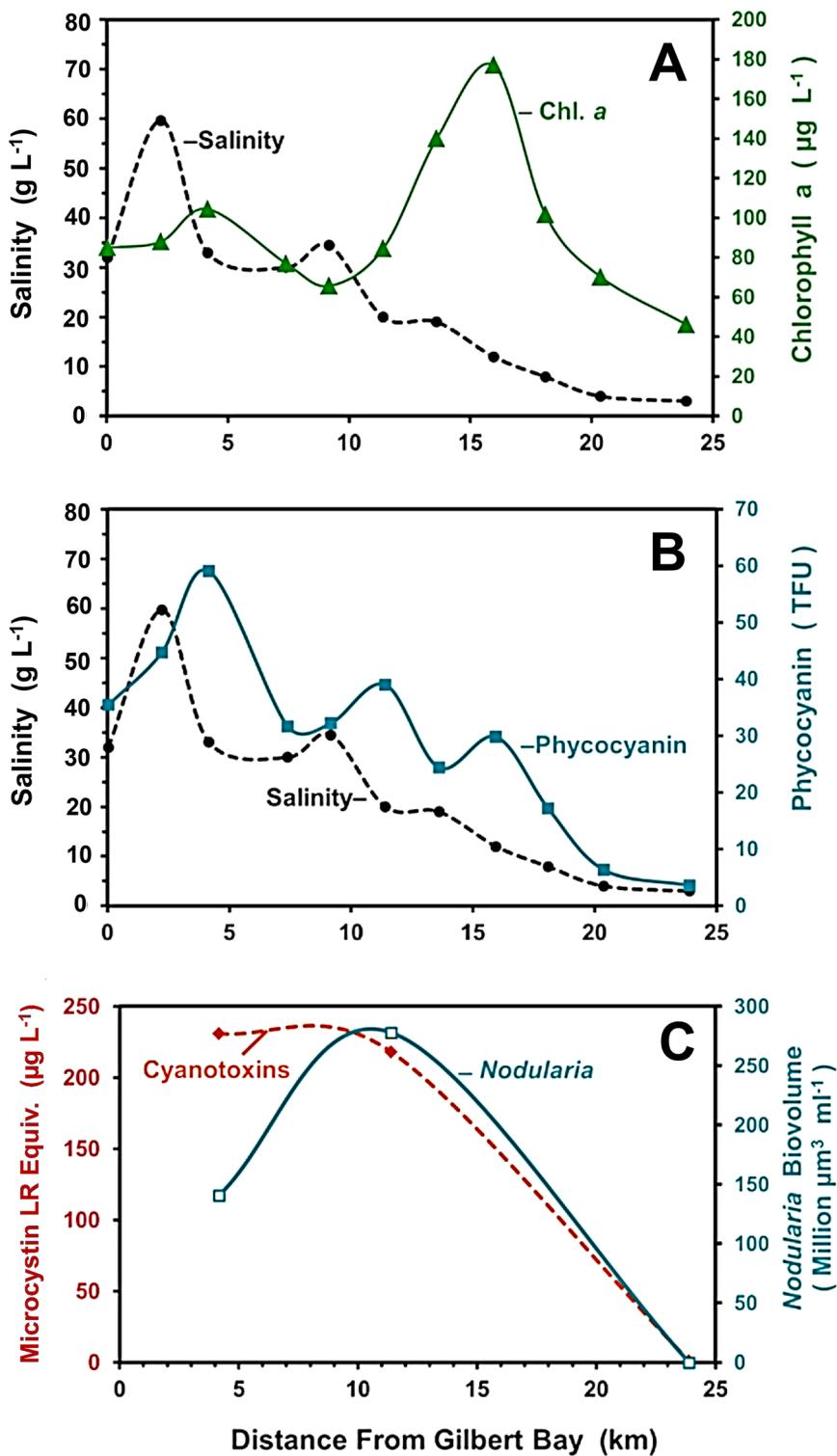


Fig. 7. Longitudinal gradients in salinity, phytoplankton, and cyanotoxins along a longitudinal transect in Farmington Bay, 17 August 2009. Station 0, at the Causeway Bridge, was at a distance of 0.01 km from Gilbert Bay and Station 6 was 24 km distant at the south end of Farmington Bay. A. Salinity and chlorophyll levels along the transect. B. Phycocyanin concentrations (in arbitrary Turner Fluorescence Units, TFU) and salinity along the N-S gradient. C. Cyanotoxins and *Nodularia* biomass (only measured at stations 1, 3 and 6). Note that we did not have replicates for these measurements.

adaptation to fluctuating salinities. In Farmington Bay we found abundant populations of *Nodularia* at salinities ranging from 8–50 g l^{-1} (Fig. 5, 7), although it is possible that advection in the bay moved populations that were growing in lower salinities to high salinities. Based on hypsographic information on Farmington Bay and mean monthly discharges of the Jordan River into the bay, the residence time is approximately 40

days, so movement through the estuary is rapid. Data from an undergraduate project (Hayes, 1971) also showed *Nodularia* at high densities in Farmington Bay at salinities ranging from 10–60 g l^{-1} , although densities peaked at 35 g l^{-1} . In the mid-1980s when Great Salt Lake reached near record high elevations and salinity in the main lake (Gilbert Bay) declined to 60 g l^{-1} , *Nodularia* were reported to be

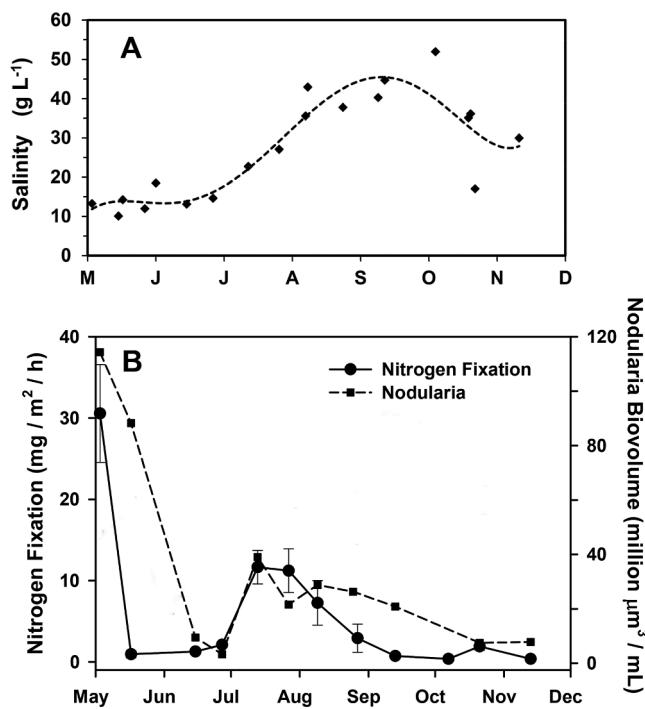


Fig. 8. A) Seasonal changes in salinity in the mixed layer at Sta. 1 in Farmington Bay during 2005. B) Seasonal pattern of nitrogen fixation and *Nodularia* biovolume in the water column (0–1.0 m) of Farmington Bay at Sta. 1 in 2005. Error bars show $\pm 1 \text{ S.E.}$, $n = 2$.

abundant there (Stephens, 1990), again suggesting a high salinity tolerance for this species, and local adaptation in this lake. During the same period, Wurtsbaugh (1988) measured significant N_2 fixation by Gilbert Bay plankton when salinities were 60–62 g l^{-1} . In culture experiments using natural plankton populations from Great Salt Lake dominated by *Nodularia*, growth was high at salinities ranging from 10–70 g l^{-1} , particularly if phosphorus was added (Marcarelli et al., 2006). Similarly, in a broad literature review Nordin (1974) reported that the maximum salinity for measurable growth of *Nodularia* was about 60 g l^{-1} , but with the optimal growth around 12–24 g l^{-1} (Nordin 1974; Blackburn et al. 1996). However, Lehtimäki et al. (1994) found that toxin production in Baltic *Nodularia* strain peaked at an intermediate salinity of only 5 g l^{-1} . Melero-Jiménez et al. (2019) demonstrated that *Microcystis* can undergo rapid genetic adaptation to increasing salinities, so it is possible that this process is also occurring in the Farmington Bay population of *Nodularia*. Additionally, the strain of *Nodularia* can have significant effects on their response to salinity (Blackburn et al., 1996), so it would be interesting to analyze Farmington Bay's *Nodularia* in pure culture to determine if they are, indeed, much more tolerant of high salinities than reported for this species elsewhere.

N_2 fixation rates in Farmington Bay were among the highest values reported for any aquatic ecosystem (Fulweiler et al., 2025; Marcarelli et al., 2022; Scott et al., 2019), consistent with the high densities of *Nodularia* we observed. The high rates also occurred at salinities greater than commonly observed elsewhere (Fig. 8). In 2005, rates as high as 2.5 $\text{mg N m}^{-2} \text{ h}^{-1}$ occurred at salinities of 35 g l^{-1} , although higher rates were measured when *Nodularia* was more abundant at lower salinities. In a culture experiment (Mazur-Marzec et al., 2005) reported that heterocysts, the site of N_2 -fixation in *Nodularia* (strain NSGG-1), nearly disappeared at salinities <3 or at greater than 35 g l^{-1} , but we observed heterocyst:vegetative ratios of 1:10 when salinities were 35 g l^{-1} in Farmington Bay. Another measurement of N-fixation in Farmington Bay on a single date in 2002 by Li et al. (2022) indicated minimal rates of <0.01 $\text{mg N l}^{-1} \text{ h}^{-1}$, where salinities ranged from 24–28 g l^{-1} . They also measured denitrification and found it to be greater than rates of fixation,

suggesting that the *Nodularia* blooms may not be a net source of N exported to the economically important Gilbert Bay, but a more detailed analysis is needed to confirm this. However, plumes of chlorophyll and/or phytoplankton stimulated by nutrient export from the bay have been observed in Gilbert Bay (Ramsey et al., 2025) and these could benefit the ecologically and economically important *Artemia* populations there.

Our results suggest that *Nodularia* should be able to grow at ocean-water salinities, although it is seldom observed there. The amount of phosphorus available for growth and N_2 fixation in Farmington Bay may allow *Nodularia* to function at high salinities. Marcarelli et al. (2006) found that when *Nodularia* were cultured in 30-day experiments, maximum N_2 fixation rates in P-addition treatments (200 $\mu\text{g P l}^{-1}$) showed no clear relationship with salinities from 10 to 70 g l^{-1} but declined to zero at salinities above 70 g l^{-1} . However, the N_2 fixation response to P additions was faster from salinities of 10–50 than at 70 g l^{-1} , suggesting that there may have been strain selection or genomic regulation (Teikari et al., 2018) that took several weeks before the *Nodularia* adapted to the highest salinity. Wurtsbaugh (1988) also found that P additions increased N_2 fixation in Gilbert Bay phytoplankton when *Nodularia* was abundant there (c.f. Stephens, 1990). Similarly, in the Baltic Sea, P inputs into the upper-mixed layer during bloom periods stimulated N_2 fixation and helped maintain the cyanobacterial blooms there (Moisander et al., 2003). Although high N concentrations may promote the overall phytoplankton community, these authors found that N additions had little, or sometimes negative effects on N_2 fixation by the *Nodularia*-dominated communities.

The high sulfate levels of the ocean have been suggested to inhibit molybdenum uptake of cyanobacteria and limit N_2 fixation because this micronutrient is a necessary co-factor for N_2 fixation (Howarth and Cole, 1985; Patiño et al., 2023). Although we did not measure sulfate or molybdenum during this study, previous bioassay results with plankton from Gilbert Bay when salinities were near 60 g l^{-1} and $\text{SO}_4:\text{Mo}$ ratios were higher than in the ocean, indicated that molybdenum did not limit N_2 fixation (Wurtsbaugh, 1988). These results suggest that salinities <70 g l^{-1} and high P levels are necessary conditions for N_2 fixation in saline environments as concluded by Marcarelli et al. (2006).

Surprisingly, we found minimal *Dolichospermum* sp., and no *Aphanizomenon flos-aquae*, or *Microcystis* in any of the bays. These taxa grow better at salinities less than those tolerated by *Nodularia* (Brutemark et al., 2015; Lehtimäki et al., 1997; Li et al., 2021; Melero-Jiménez et al., 2020; Wulff et al., 2018). A reanalysis of the data of Olofsson et al. (2020) indicated that *Dolichospermum* and *Aphanizomenon* biovolumes across the entire Baltic Sea were independent of salinities ranging from 4–8 g l^{-1} , whereas the biovolume of *Nodularia* increased significantly (13-fold; $p < 0.001$) over this range. Consequently, it was not surprising that *Nodularia* dominated in the parts of Farmington Bay we usually sampled where salinities were almost always greater than 10 g l^{-1} (Fig. 2A). However, on our single transect in Farmington Bay and in certain seasons in Bear River Bay, salinities near the river inflows were in a range reported to be tolerated by *Dolichospermum*, *Aphanizomenon*, and *Microcystis*, yet they were nearly all absent. We hypothesize that the lack of *Dolichospermum* and *Aphanizomenon* in the lower salinity water was due to the high dissolved inorganic nitrogen (DIN) in the effluent and river inflows to these bays that mitigate the advantage N_2 fixers have over other algal taxa, potentially resulting in a lower abundance in those areas. For example, average DIN concentrations at the south end of Farmington Bay near the Sewage Canal were near 0.40 mg l^{-1} (Li et al., 2022; McCulley et al., 2015). Nevertheless, DIN was sometimes high in the northern part of Farmington Bay where *Nodularia* flourished (McCulley et al., 2015), so additional work is needed to understand the interaction between nitrogen forms and the abundances of these species. Similarly, *Microcystis*'s ability to withstand salinity is highly dependent on the availability of N, where high N availability decreases its salinity tolerance (Li et al., 2021). Cell growth and cyanotoxin production in this common species generally stops at salinities >10–18 g l^{-1} and is lower at

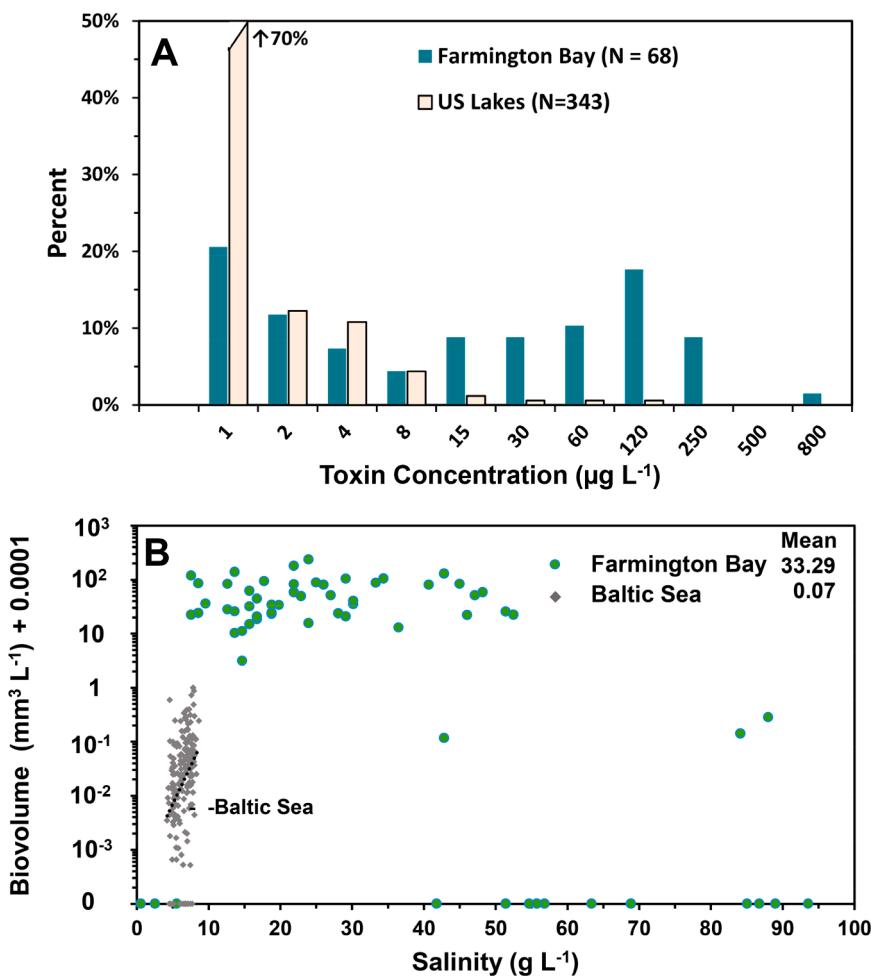


Fig. 9. A) Distribution of microcystin concentrations in U.S. lakes during the EPA 2017 National Lake Assessment (U.S. Environmental Protection Agency, 2017), and nodularin concentrations in our Farmington Bay samples based on PPIA analyses. Toxin concentrations below detection ($0.15 \mu\text{g l}^{-1}$) were not included in the distributions (US lakes, $n = 748$; Farmington Bay, $n = 68$). B) Comparison of *Nodularia* biovolumes in Farmington Bay (GSL) with those in the Baltic Sea ($N = 207$). Note the near absence of *Nodularia* in Farmington Bay at salinities $< 6 \text{ g l}^{-1}$ and $> 55 \text{ g l}^{-1}$. Baltic Sea data are from Olofsson et al. (2020). The regression for the Baltic cell biovolumes is: $\text{Log Biovolume} = 0.2806 * \text{Salinity} - 3.5552$; $p < 0.001$.

high dissolved N concentrations and this may explain its low occurrence in the Bay.

4.3. Productivity, invertebrates, bird use and human impacts

Because Great Salt Lake is a terminal lake that retains nutrients and millions of people discharge nutrients into the system, it is highly productive (Ramsey et al., 2025) with planktonic chlorophyll levels in all three bays reaching above $50 \mu\text{g l}^{-1}$ and attaining a mean level of $141 \mu\text{g l}^{-1}$ in Farmington Bay (Fig. 2B). Visual observations indicate that benthic algal levels are also high, although they have only been measured on the microbiolite communities in Gilbert Bay (Wurtsbaugh et al., 2011). Submerged and emergent macrophytes are also abundant in the freshwater sections of Bear River and Farmington Bays, contributing to the overall high productivity. Benthic invertebrate abundances are high as well, with the mean biomasses of 3.1, 3.3, and 5.6 g m^{-2} in Farmington, Bear River and Gilbert Bays (Armstrong and Wurtsbaugh 2019; Gilbert Bay invertebrate biomass derived from Collins (1980) and Wurtsbaugh et al. (2011)). The high abundance of benthic invertebrates and brine shrimp attracts millions of shorebirds and waterfowl to the lake (Conover and Bell, 2020; Paul and Manning, 2002; Tavernia et al., 2023). These feed on brine shrimp and brine flies (*Ephydria cinerea*) in Gilbert Bay, and on a variety of benthic and pelagic invertebrates in Farmington and Bear River Bays (Armstrong and Wurtsbaugh, 2019;

Roberts, 2013; Wurtsbaugh et al., 2011). Fish and piscivorous pelicans, grebes and herons are also abundant in the fresher sections of Farmington and Bear River Bays (Armstrong and Wurtsbaugh, 2019; Paul and Manning, 2002).

Although the elevated productivity supports high bird densities, cyanobacterial toxins have also been shown to cause flamingo, duck, and bald eagle mortalities with cyanobacterial densities far less than those in Farmington Bay (Alonso-Andicoberry et al., 2002; Matsunaga et al., 1999; Wilde et al., 2005). Nodularin and microcysts do not biomagnify, but they do bioaccumulate in the food chain (Ferrão-Filho and Kozlowsky-Suzuki, 2011; Glidewell et al., 2025). Rattner et al. (2022) recently reviewed the impacts of cyanobacterial blooms on birds and suggested that deaths were infrequent. However, multiple bird mortalities (waterfowl, shorebirds, and gulls) were associated with *Microcystis* blooms in eutrophic ponds located on an island in their principal study site, Chesapeake Bay (USA), where microcystin concentrations as high as $46,000 \mu\text{g l}^{-1}$ were reported (presumably from scums). López-Rodas et al. (2008) reported a significant die-off of fish and over 6000 birds of 47 species in Doñana National Park (Spain) that was linked to a bloom of *Microcystis*. Piscivorous birds that died had high concentrations of microcystin in their livers, suggesting that bioaccumulation was an important mechanism in their deaths. Toxic cyanobacterial blooms have been associated with, and suspected of, causing mortalities and initiating botulism in other aquatic bird populations

(Murphy et al., 2000, 2003). However, a direct cause and effect relationship between cyanobacterial densities and botulism has yet to be established. Massive botulism-caused mortalities in both Farmington and Bear River Bays are largely unexplained, so more work is needed to understand this problem, especially considering the magnitude of blooms in Farmington Bay.

The *Nodularia* blooms in Farmington Bay are also a potential health issue for humans. However, the bay is not used as a drinking water source and is used minimally for contact recreation. The primary contact recreation is by waterfowl hunters in the fall, and during our study, blooms had subsided by then. Another potential problem is cyanotoxin dust exposure from the dry lakebed on the nearby population center of Salt Lake City, but dust impacts on residents has only recently received attention (Abbott et al., 2023; Grineski et al., 2024; Metcalf et al., 2023, 2012).

4.4. Current conditions

Since our study, the Great Salt Lake's elevation decreased 1.5 m due to water diversions and an extended drought, reaching a record low elevation of 1277.1 m in 2022. This effectively isolated Farmington and Bear River Bays from the larger and saltier Gilbert Bay and greatly decreased the areas of the two smaller bays. Farmington Bay essentially became a shallow, broad, fresher river with salinities ranging from 4 g l⁻¹ in the south to 28 g l⁻¹ in the north (Armstrong and Wurtsbaugh, 2019) and sampling on a single date in 2020 indicated that *Nodularia* was still present in the north (Li et al., 2022). The lake has risen some due to increased precipitation and efforts to restore diverted water to the lake. If Gilbert Bay reconnects with Farmington Bay and salt water intrudes there, the large blooms of *Nodularia* we documented will likely return. Although a higher overall lake level is badly needed, this will require water quality managers to address the cyanobacterial blooms in Farmington Bay.

5. Conclusions

Toxic cyanobacterial blooms can cause problems for recreation, drinking water production, and harm to the natural ecosystem. Eutrophication may significantly increase the risk of such blooms, and understanding the factors controlling it in saline lakes is therefore important, especially since these systems provide various ecosystem services. Our study demonstrated that salinity is a major controlling factor for blooms of *Nodularia spumigena* in one of Great Salt Lake's bays that receives high nutrient loading. This species and its toxin, nodularin, reached extreme levels at salinities ranging from 8–50 g l⁻¹, which are much higher than usually tolerated by this taxon. This knowledge furthers our understanding of salinity adaptation and the potential spread of this species to new regions. *Nodularia*'s salt-tolerant traits are thought to be plastic, but it would be interesting to compare the genomes of *Nodularia* from the Great Salt Lake with strains from other waterbodies such as the Baltic Sea where it has been intensively studied to determine whether there are strains uniquely adapted to different salinities.

While the N₂ fixation and growth of *Nodularia* in Farmington Bay contributes to high production that supports resident and migratory bird populations, the benthic invertebrates on which the birds feed are lower than in the two other less eutrophic bays we studied. The high nodularin levels are potentially detrimental to the birds and prohibits human contact recreation in the bay. Cyanotoxins in dust blown from the lake's playas also reach the population center of greater metropolitan Salt Lake City. While some of these problems have been alleviated due to the desiccation of the bay, water quality managers will need to address the harmful algal blooms if in the future Great Salt Lake returns to higher levels.

CRediT authorship contribution statement

W.A. Wurtsbaugh: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Malin Olofsson:** Writing – review & editing, Visualization, Methodology, Investigation. **Gregory L. Boyer:** Writing – review & editing, Methodology, Investigation. **Amy M. Marcarelli:** Writing – review & editing, Visualization, Methodology, Investigation.

Declaration of competing interest

The authors declare no competing interests.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2025.102959.

Data availability

Data will be made available on request.

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