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ARTICLE

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

Abstract: Saline lakes change in size and salinity because of natural climate variability and especially from inflow diversions, which threaten life in these waters. We conducted a microcosm experiment in 12 L containers using organisms from the Great Salt Lake to determine how salinities ranging from 10 to 275 g·L^{-1} influenced the ecosystem. After 30 days, brine shrimp (*Artemia franciscana*) were nearly absent in salinities of 10 g·L^{-1} (where fish survived) and >225 g·L^{-1}. As salinities increased from 75 to 225 g·L^{-1}, final masses decreased 60% and their total biomass decreased fourfold. Copepod and rotifer biomasses were negligible at salinities >50 g·L^{-1}. Brine fly (*Ephydra gracilis*) final biomass decreased 45% as salinity increased from 50 to 250 g·L^{-1}. When *Artemia* and other grazers were abundant, phytoplankton chlorophyll levels were near 4.0 μg·L^{-1}, but when grazing rates declined at higher salinities, phytoplankton chlorophyll increased to 130 μg·L^{-1}. Mean periphyton chlorophyll levels showed the reverse pattern. Denitrification decreased total N concentrations during the experiment, resulting in final N:P ratios indicative of algal nitrogen limitation. The microcosm experiment demonstrated the strong influence of salinity on the entire ecosystem and highlighted the need for careful management of salt lakes to maintain appropriate salinities.

Résumé : La taille et la salinité des lacs salins changent en raison de la variabilité naturelle du climat et, particulièrement, des déviations des apports d'eau, qui menacent la vie dans ces plans d'eau. Nous avons mené une expérience en microcosme dans des contenants de 12 l en utilisant des organismes tirés du Grand lac Salé pour déterminer l'influence sur l'écosystème de salinités allant de 10 à 275 g·L^{-1}. Après 30 jours, les artémies (*Artemia franciscana*) étaient presque absentes à des salinités de 10 g·L^{-1} (dans laquelle survivaient les poissons) et de >225 g·L^{-1}. L'augmentation de la salinité de 75 à 225 g·L^{-1} était associée à une réduction de 60 % des poids finaux et une diminution par un facteur de quatre de leur biomasse totale. Les biomasses de copépodes et de rotifères étaient négligeables à des salinités de >50 g·L^{-1}. Une réduction de 45 % de la biomasse finale des mouches *Ephydra gracilis* a été observée pour une augmentation de la salinité de 50 à 250 g·L^{-1}. Quand les *Artemia* et autres brouteurs étaient abondants, les teneurs en chlorophylle du phytoplancton approchaient 4,0 μg·L^{-1}, mais quand les taux de broutage baissaient à salinité plus élevée, la chlorophylle du phytoplancton augmentait à 130 μg·L^{-1}. Les teneurs moyennes en chlorophylle du périphyton présentaient une distribution inverse. La dénitrification réduisait les concentrations en N total durant l'expérience, produisant des rapports N:P finaux témoignant d'une limitation de l'azote algal. L'expérience en microcosme démontre la forte influence de la salinité sur tout l'écosystème et souligne la nécessité d'une gestion soigneuse des lacs salins afin d'y maintenir des salinités adéquates. [Traduit par la Rédaction]

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 (*Trichocorixa 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 because of 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 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

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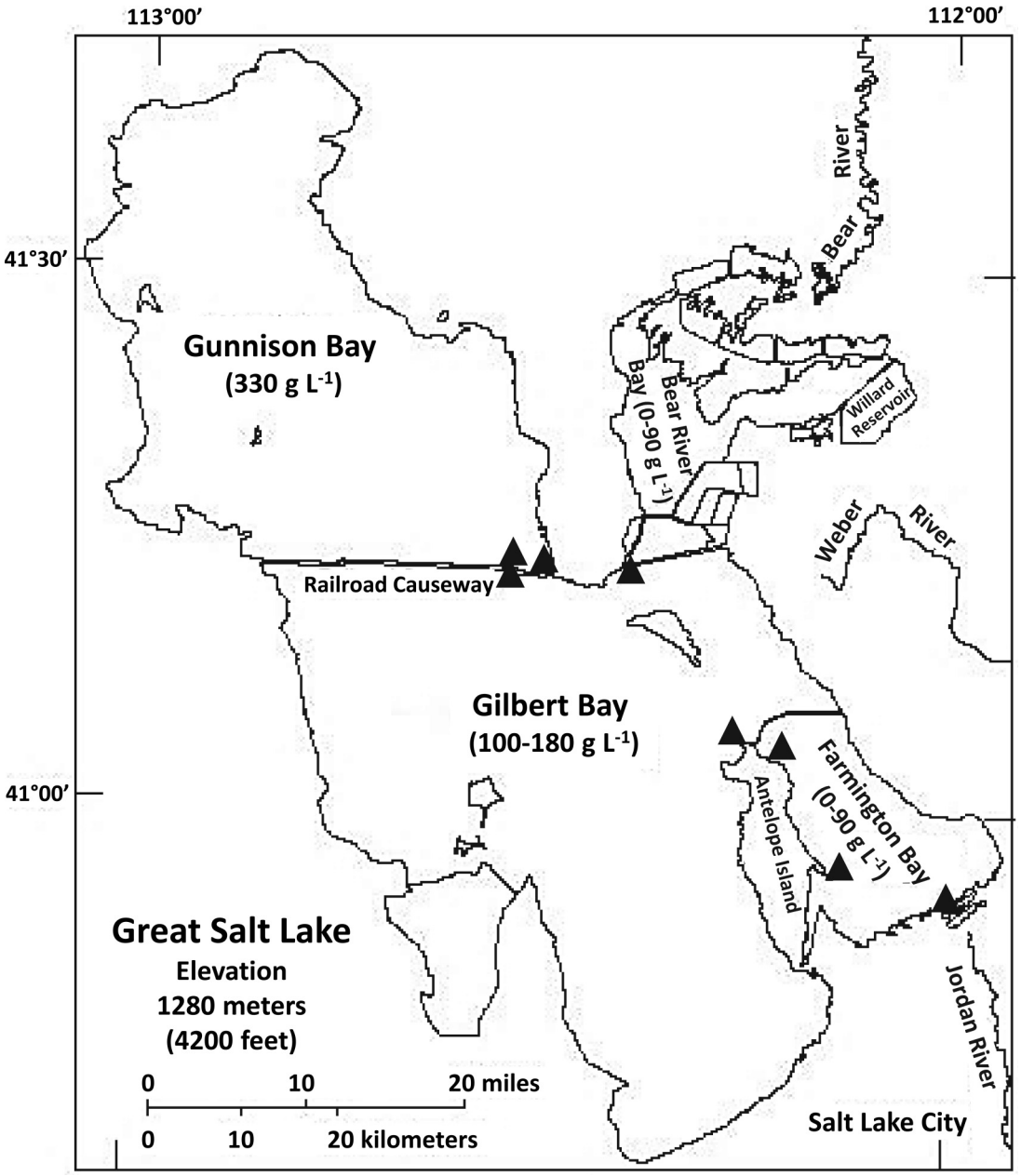
Fig. 1. Map of the Great Salt Lake showing its four bays with common salinity ranges in each. Triangles indicate areas where water, organisms, and sediments were collected to seed the experimental microcosms.



Great Salt Lake, Utah, 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 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 to 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 to 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 (~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). Owing 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 multimillion 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.

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

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

	Great Salt Lake		Microcosm experiment (nominal salinities, g·L^{-1})					
Major ions	Gunnison Bay	Gilbert Bay	10	50	100	150	200	250
Na^+	0.320	0.313	0.350	0.330	0.307	0.314	0.313	0.320
K^+	0.026	0.027	0.017	0.025	0.024	0.025	0.024	0.025
Mg^{+2}	0.032	0.035	0.037	0.020	0.017	0.016	0.016	0.016
Ca^{+2}	0.001	0.002	0.004	0.001	0.001	0.001	0.001	0.001
Cl^-	0.554	0.551	0.502	0.538	0.571	0.562	0.563	0.562
SO_4^{-2}	0.067	0.073	0.090	0.086	0.080	0.082	0.083	0.076

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, plankton, sediment, and macroorganisms from the Great Salt Lake collected from four sites (Fig. 1; Supplemental Table S1[1]) 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 the middle of 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 *T. 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 h light : 12 h 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 mass. This mixture yielded an ion concentration similar to that of 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·s^{-1}. Buckets were covered with 1.6 mm mesh screen lids to prevent unwanted colonization and escape of emerging insects, and a 3 cm × 3 cm × 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 1-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 h 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 h light : 8 h 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·L^{-1} as Na_2HPO_4; 700 μg N·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 J.W. Gwynn (unpublished):

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

After 3 days of algal growth, sediment was added to each microcosm. This day will be referred to as Day 0 (15 March 2013). A homogeneous mixture of moist sediment from each locale described above was added by mass (500 g), providing approximately a 1 cm thick sediment layer in each bucket.

Zooplankton were added to each microcosm 1–2 h 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

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0396.

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 *T. 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 Days 1 or 2. The second and third instar *Ephydra* (only *Ephydra gracilis* were found in the initial samples) larvae that had been collected from Gilbert Bay were acclimatized by raising the temperature ~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 2 h, 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 with 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 nonacidification method of Welschmeyer (1994) on a Turner 10AU fluorometer. Phycocyanin pigment, an indicator of cyanobacterial biomass, was analyzed in samples of raw water from each bucket with the Turner 10AU fluorometer and Turner's phycocyanin optical kit that utilizes narrow-band interference filters with excitation and emission wavelengths of 630 and 660 nm, respectively.

On Day 30 of the experiment, zooplankton and "benthic" organisms in the water column were sampled by pouring ~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× 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 taxon were estimated by measuring lengths at 10–30× magnification with a microscope and converting these to mass using length–mass 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 10AU fluorometer as described above.

Table 2. Nominal and mean (N = 2) measured salinities of the microcosm treatments over the course of the experiment.

Nominal salinity (g·L^{-1})	Mean salinity (g·L^{-1}) ± SD	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

Note: The salinities are given as either grams per litre or percent. Equation 1 was used to convert between the two types of units.

Statistical analyses

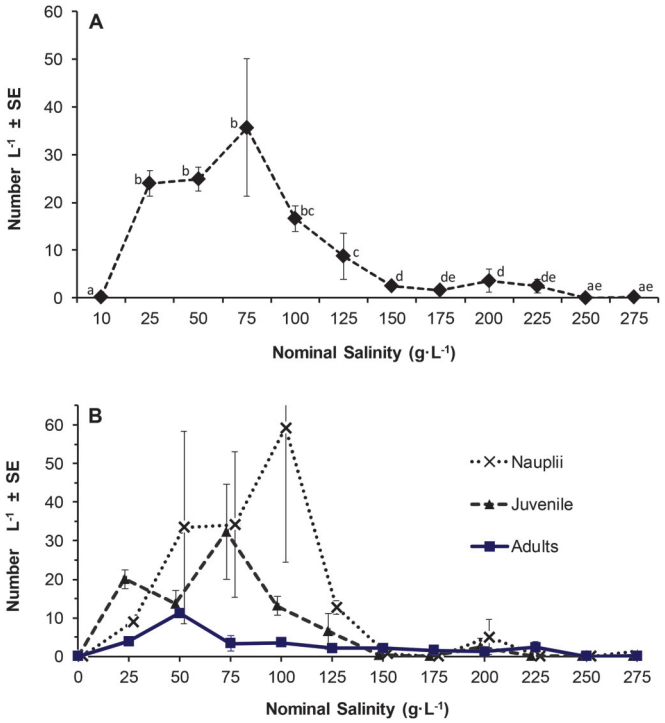
Because most parameters responded markedly to the different salinity treatments and because variability was often high between replicates, we used $\log_{10}$ transformations to equalize variances. Most analyses were done as one-way analyses of variance followed by Fisher's least significant difference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

Results

Densities of organisms

Final densities of juvenile plus adult *Artemia* in the microcosms were significantly influenced by salinity (one-way ANOVA, $p < 0.001$; Fig. 2A). No *Artemia* were found in the 10 g·L^{-1} treatment where fish were present (see below). At salinities ranging from 25 to 100 g·L^{-1}, densities were very high (17–35·L^{-1}) and not statistically different (LSD; $p > 0.11$). At 125 g·L^{-1} *Artemia* densities decreased substantially 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 fewer 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

Fig. 2. (A) 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.



salinities (above 150 g·L^{-1}), almost all were adults, while lower salinities were composed 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.

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 (*Monostyla* sp., length = 0.1 mm) 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* were only abundant in one 25 g·L^{-1} replicate where they reached 4.4 individuals·L^{-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 density. 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. 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 *Ephydra hians* pupae found in a 75 g·L^{-1} treatment. Our initial control subsample contained no *E. hians*, which are found at very low proportions compared with *E. gracilis* in the Great Salt Lake (Collins 1980), 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

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

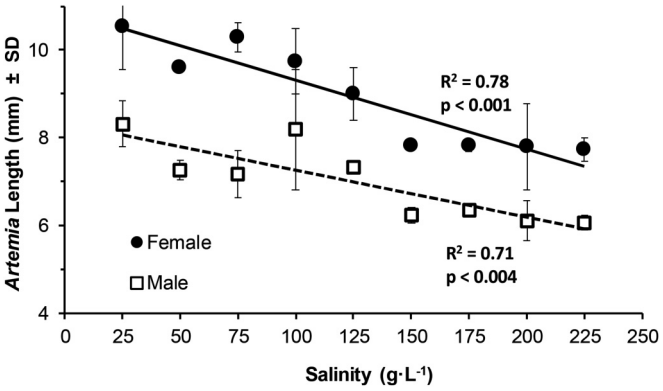
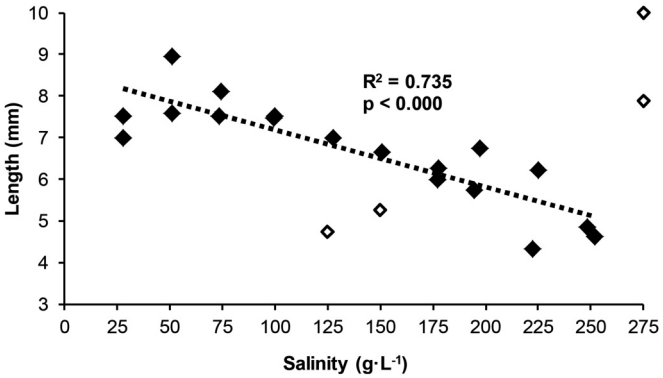


Fig. 4. Mean lengths of *Ephydra* larvae (n = 10) in each replicate of the different salinity treatments on the final day of experiment. Microcosms with fewer than four individuals to sample (open symbols) were not included in the regression.

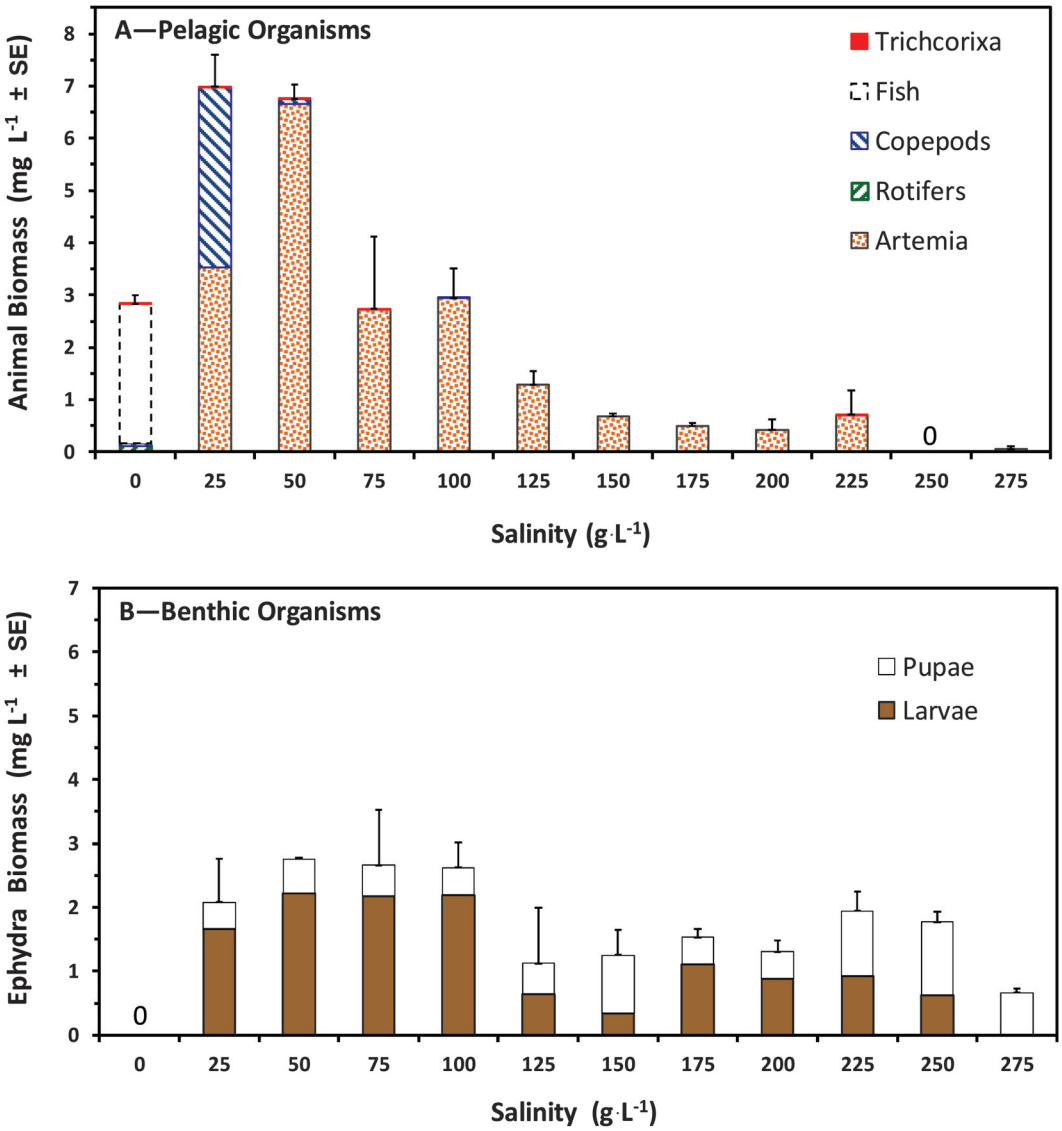


the water surface during the experiment, generally 1–2 days after the fresh water was added, but no more than four adults emerged in a single microcosm, and none survived to the final day of the experiment. Several larval chironomids were observed in the 10–25 g·L^{-1} treatments on Days 1–3 of the experiment, but none were observed after Day 4. *Gambusia* only survived in the 10 g·L^{-1} treatment, with densities of one per microcosm.

Species lengths and community biomass

Just as salinity impacted *Artemia* densities, salinity exerted considerable limitations on *Artemia* growth. Mean adult *Artemia* lengths were reduced by approximately 30% (Fig. 3) from the lowest salinity in which they survived (25 g·L^{-1}) to the highest salinity (225 g·L^{-1}). The mean 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 mean length of inoculated adult males 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 (Fig. 3). The linear decrease in mean length with increasing salinities translated to nearly a threefold decrease in the mean estimated mass of an adult *Artemia*. In salinities of 25–50 g·L^{-1} *Artemia* averaged 680 μg·individual^{-1}, whereas in salinities of 200–225 g·L^{-1} they averaged only 230 μg·individual^{-1}. Similar to the effect on *Artemia*, increased salinities decreased the growth and final masses of *Ephydra* in the microcosms, but not their densities. The mean length of *Ephydra* larvae in the inoculum was 6.0 mm. Mean final *Ephydra* larvae length was almost 40% less at the higher salilnities than at the lower salinities (Fig. 4). Larvae in 25–75 g·L^{-1}

Fig. 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 in the salinity treatments. Error bars show +SE of the total biomasses at each salinity.



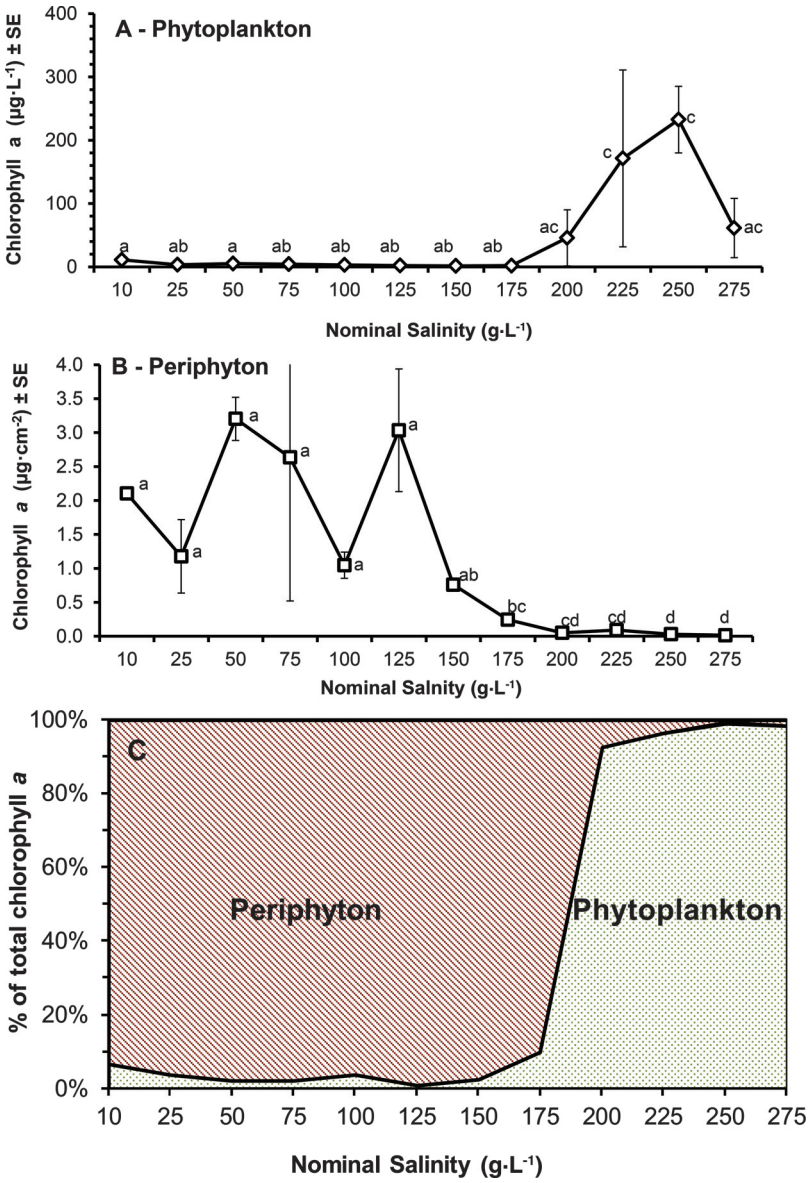
salinity treatments had a mean length of 7.5 mm, while those in 200–250 g·L^{-1} averaged 5.5 mm. There was no major change in *Ephydra* pupae length. The shorter larval lengths resulted in a calculated decrease in the mean mass of individuals from approximately 1.1 to 0.6 mg over the salinity range.

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). Final zooplankton biomass was only 0.2 g·L^{-1} (dry mass) 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 mass of 0.12 g to a mean of 0.15 g wet mass and represented a mean biomass of 2.7 mg dry mass·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}. *Trichocorixa 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).

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 because of dense population with large adults and juveniles in both replicates (Fig. 2A). The 25–100 g·L^{-1} salinity treatments contained mean *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 mass of individuals.

Since *Ephydra* were the only benthic macroorganisms found, 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 becaue of the persis-

Fig. 6. (A) 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, $p > 0.05$).



tence of brine flies from the initial inoculation, as *Ephydra* may not be able to reproduce at the highest salinities we tested.

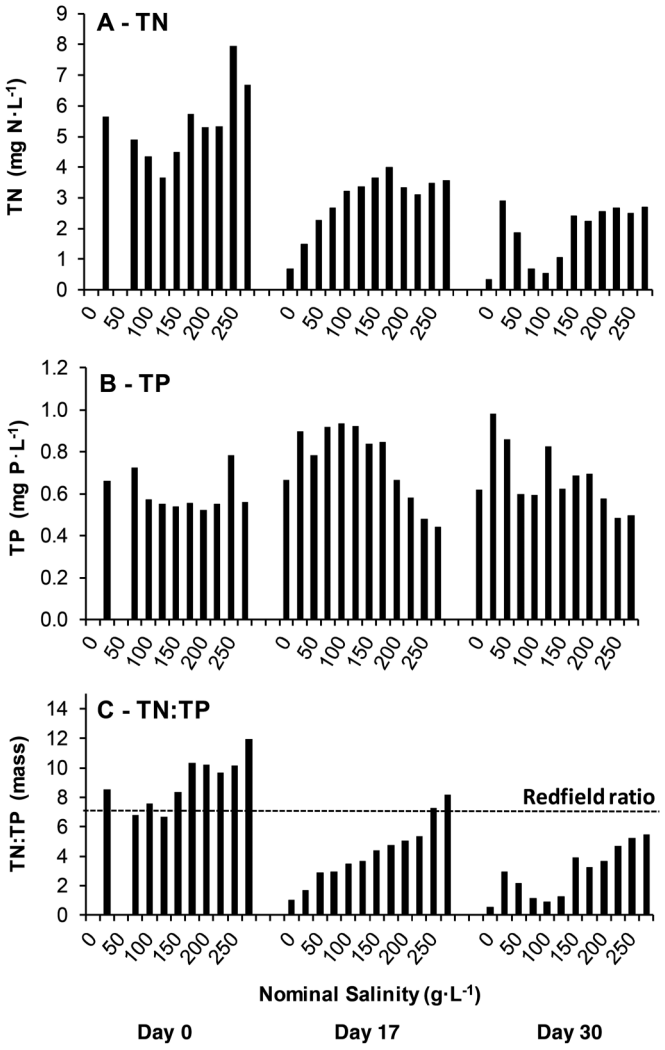
Chlorophyll in phytoplankton and periphyton

Both time and salinity had significant effects on measured chlorophyll *a* levels in phytoplankton (two-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·L^{-1} in salinity treatments less than 200 g·L^{-1} where more grazing zooplankton were present, while phytoplankton chlorophyll levels had risen to 27–49 µg·L^{-1} in salinity treatments from 200 to 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). In the 10 g·L^{-1} salinity treatment where *Artemia* were absent, mean chlorophyll levels were 11 µg·L^{-1}, but in the 25–175 g·L^{-1} treatments where *Artemia* 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, because of 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 sixfold at a salinity of 125 g·L^{-1} 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).

Salinity also affected the distribution of algal biomass between phytoplankton (pelagic) and periphyton (benthic). Chlorophyll *a*

Fig. 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 panel C shows the Redfield ratio of balanced nutrient levels for average phytoplankton.



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 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 (two-way ANOVA without replication; time, $p < 0.000$; salinity, $p < 0.019$). TP 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 ($p < 0.000$).

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.

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 from 48 h LC_{50} bioassays reported by Barnes and Wurtsbaugh (2015), 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 that 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 to 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 consistent with 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 considerably 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 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 mg·L^{-1} (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 (DeWachter 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}.

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 a mean 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, grazing rates by zooplankton are reduced. 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}, 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 *Dunaliella 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^{-1}; Wurtsbaugh and Marcarelli 2006) of the predator *T. 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·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 h LC_{50} bioassays (Barnes and Wurtsbaugh 2015) support the conclusion that brine fly larvae can survive at salinities as high as 275 g·L^{-1} for at least 1 month. Because brine flies are believed to grow from egg to pupae in 3–4 weeks and spend 2–3 weeks as pupae (Collins 1980), 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 with those in the innocula suggests that substantial 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}, *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 to 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 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 microcosms experiments were two of the more distinct responses to the salinity treatments. Although TN 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 mol·L^{-1} 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 (anaerobic ammonium oxidation) — 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 mass (8.8:1 in molar concentration), 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; Caraco et al. 1989). 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. E. Ogata, W. Wurtsbaugh, and T. Smith (unpublished data) found that the combination of nitrogen limitation and high grazing pressure by *Artemia* substantially reduced phytoplankton abundance in a 2-week nutrient addition bioassay.

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 owing 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 $g \cdot L^{-1}$ in our experiment, the aquaculture industry at the Great Salt Lake prefers salinities near 150 $g \cdot L^{-1}$, 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 salinities that are 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 Great Salt Lake 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 because of 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 1971; 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.

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