

Salinization decreases population densities of the freshwater crustacean, *Daphnia dentifera*

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Abstract Salinization of freshwater systems is a global concern. In the northern United States, a large driver of freshwater salinization is the application of road salt which runs into freshwater systems. We tested the effects of salinization on traits and population densities of the freshwater crustacean, *Daphnia dentifera*, a common species in the Midwestern United States. We first measured the effects of salinity on resource acquisition (feeding rates), birth rates, and death rates of individual *D. dentifera*. Then we performed an experiment to quantify the population-level effects of salinity. There was little effect of salinity on individual characteristics; birth and death rates were unaffected by salinity treatment and only

one *D. dentifera* genotype showed lower feeding rates with increased salinity. However, *D. dentifera* population densities were lower with increased salinity. Our results suggest that studies conducted on individuals may underestimate the population-level effects of salinization. Moreover, since *Daphnia* are often dominant grazers in freshwater systems, reduced population densities from salinization could have dramatic effects on communities and ecosystems.

Keywords Experimental scale · Midwestern USA · Road salt · Salinity · Saline · Zooplankton

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Introduction

Dramatic changes to freshwater systems are occurring on a global scale (Carpenter et al., 1992, 2011). For example, runoff of toxins and wastes from terrestrial environments (Hanazato, 2001; Smith et al., 1999) and alterations to water flow (including river damming or water diversion; Ligon et al., 1995; Bunn & Arthington, 2002) are having large impacts on freshwater systems. These human-induced changes are widespread and can have numerous effects on communities and ecosystems.

One widespread concern in freshwater systems is salinization (Williams, 2001; Nielsen et al., 2003; Kaushal et al., 2005). Land use changes, discharge of agricultural wastewater, and alterations to water flow can all increase freshwater salinity (Williams, 2001).

Additionally, runoff from roads treated with de-icing solution (road salt) can contribute to salinization in areas with harsh winters (Peters & Turk, 1981; Rosenberry et al., 1999; Godwin et al., 2003; Corsi et al., 2015). In the United States alone, an estimated 10–20 million tons of road salt are used each year (Kelly et al., 2010), creating substantial runoff into freshwater environments. Chloride concentrations in streams around the northeastern United States, where road salt is commonly applied throughout the winter months, can reach over 4.5 g l^{-1} (equivalent to 25% of the concentration of seawater; Kaushal et al., 2005). Thus, road salt can be a major driver of freshwater salinization.

Salinization can have numerous effects on aquatic organisms including changes to physiology (Morgan & Iwama, 1991; Cheng & Chen, 2000), population growth (Sarma et al., 2006), and community structure (McKee & Mendelsohn, 1989; Alcaraz et al., 2008). For example, in some species of *Daphnia*, increasing salinity has been shown to reduce individual growth rates, decrease respiration, lower fecundity, and increase mortality (Arnér & Koivisto, 1993; Hall & Burns, 2002; Martínez-Jerónimo & Martínez-Jerónimo, 2007). In stratified lakes inhabited by *Daphnia* in the Midwestern United States, chloride concentrations have been found to be up to 13 times historic levels (Bridgeman et al., 2000). However, the majority of studies investigating the effects of salinity on freshwater organisms focus on individuals. Less is known about how salinization influences population dynamics.

We investigated the effects of salinization on *Daphnia* at both the individual and population levels. We chose to focus on *Daphnia dentifera* Forbes, a dominant grazer in stratified lakes of the Midwestern USA (Hebert, 1995; Tessier & Woodruff, 2002) because road salt is commonly applied throughout much of its range. The effects of salinity on *D. dentifera* traits and population densities are unknown. Since *D. dentifera* are primary consumers of algae and detritus, and are important food sources for a variety of predators (e.g., young fish and insect larvae), changes to *D. dentifera* populations may influence the entire lake community. Using a series of laboratory experiments, we sought to understand how increased salinity, at levels found in the natural range of *D. dentifera*, can affect *D. dentifera* individuals and populations. We predicted that higher salinity would

decrease *D. dentifera* reproduction and feeding rates in individual-level experiments, and reduce population densities in a population-level experiment.

Materials and methods

Salinity levels and field collection

All our experiments used two salinity levels: (1) control, which is similar to the salinity of most inland lakes in the northern United States (high hardness COMBO media; Baer & Goulden, 1998; Supplemental Materials), and (2) “high salt” (0.60 g l^{-1} NaCl dissolved in COMBO media). The high salt condition was chosen to match that of Third Sister Lake (Washtenaw County, Michigan, USA), which has experienced increased salinity due to residential and commercial development in its catchment area (Bridgeman et al., 2000). The increase in salinity has caused the lake to become meromictic (Judd et al., 2005). We measured specific conductivity in Third Sister Lake and 11 other lakes in April 2014, which was shortly after the lakes thawed (Fig. S1). A previous study found that Third Sister Lake’s specific conductivity peaked shortly after snow melt (Judd et al., 2005). *Daphnia* were present in the lake at this time, but at low densities. *D. dentifera* abundance in most Midwestern lakes is low immediately after snow melt and peaks in the late summer (Duffy & Hall, 2008). We matched our high salt treatments to mimic conductivity levels from Third Sister Lake at this time ($1583 \mu\text{S cm}^{-1}$ at 6.01°C) which likely represents the peak salinity level that *D. dentifera* would experience in this lake. Conductivity of the 11 other sampled lakes was much lower than in Third Sister Lake ($444 \mu\text{S cm}^{-1}$ at approximately 6°C) and close to that of our control treatments (see Supplement for details). *Daphnia dentifera* were collected from lakes in Indiana and Michigan, USA, using a Wisconsin net. None of the lakes where *D. dentifera* were collected has a history of salinization.

Individual-level experiments

We first performed a series of experiments to measure the effects of salinity on *D. dentifera* birth, death, and feeding rates. Experiments were conducted at 20°C with a 16:8 light:dark photoperiod in Geneva

Scientific GSI-41VL incubators with four 32 W fluorescent bulbs. *Daphnia dentifera* were kept in individual 50 ml beakers filled with 30 mL of their treatment water unless noted. Each animal was fed daily with 1.0×10^6 cells of the nutritious alga *Ankistrodesmus falcatus* (Corda) Ralfs (3.3×10^4 cells ml^{-1} in the experimental containers). All experiments had a 2×5 experimental design with two salinity treatments (control vs. high salt) and five *D. dentifera* genotypes; each from a different lake to ensure we were testing a diverse group of genotypes (Table S1).

Our first experiment measured the effects of salinity on *D. dentifera* birth and death rates. We placed 1–2-day-old *D. dentifera* in individual beakers with either control or high salt solutions. Each genotype \times salt treatment combination was replicated 15 times. Salt was added to individual beakers to create the appropriate salinity treatments. For 30 days, we checked for mortality and offspring production every 2–3 days. Animals were moved to clean beakers with the appropriate salt concentration weekly. We estimated instantaneous birth rate (b) and background mortality rate (d) for each genotype following methods in Bertram et al. (2013, supplemental methods). The birth rate parameter requires estimating both instantaneous per capita population growth rate (r) and d . Since $r = b - d$, birth rate is the sum of r and d . This method provides us with one value for each genotype. We compared instantaneous birth rate (b), per capita population growth rate (r), and death rates (d) between salt treatments using paired Student's t -tests.

The second experiment measured the effects of salinity on feeding rates. We placed 1–3-day-old *D. dentifera* into individual beakers with the appropriate salinity (control or high salt) for 6 days. There were 10 replicates per genotype \times salt treatment. Then, we conducted a feeding assay following methods by Penczykowski et al. (2014). Briefly, each individual was placed into 10 mL of COMBO media (of the appropriate salinity) containing 10,000 cells *A. falcatus* ml^{-1} and allowed to graze for 3 h. We also established ungrazed controls with algal concentrations ranging from 0 to 12,500 cells ml^{-1} with both control and high salt concentrations. Using a Trilogy fluorometer (in vivo module, Turner Designs, Sunnyvale, CA, USA), we measured raw fluorescence of the grazed and ungrazed water. There was no effect of salt

treatment on fluorescence in the ungrazed replicates. We created standard curves pooling ungrazed replicates from control and high salt treatments. Using these standard curves, we then calculated the number of cells consumed per hour for each grazed replicate. Additionally, we measured the length of each individual (age 7–10 days) from the middle of the eye to the base of the tail. Feeding rates were not normally distributed, so they were log-transformed prior to analysis. We performed two-way ANOVAs comparing body size and log-transformed feeding rates among genotypes and salt treatments. Significant interactions were followed by a Tukey's test to identify which means were significantly different from one another.

Population-level experiment

We performed a population-level experiment to investigate the effects of salinity on *D. dentifera* population density. There were two treatments: control or high salt (described above) each replicated nine times. We filled indoor containers (18.9 l plastic buckets) with 15 l of the appropriate solution; again, salt was added individually to buckets. Each bucket was seeded with 2.5×10^8 cells of *A. falcatus*, creating a concentration of 1.6×10^4 cells ml^{-1} in the buckets. Average temperatures in the laboratory were 24.9°C (± 1.86) with a 16:8 h light:dark photoperiod created by mounting two Sylvania “cool white” Octron Ecologic 32 W bulbs directly over each bucket. We initiated each bucket with 45 individual *D. dentifera* from nine different genotypes (5 individuals per genotype). We used the same five *D. dentifera* genotypes used in the previous experiments, plus four additional genotypes (Table S1). Salt concentrations were established before addition of the algae or *D. dentifera* by creating a 100 g l^{-1} NaCl solution dissolved into COMBO media and adding 90 ml of this solution to each bucket. Control treatments received an addition of 90 ml regular COMBO media (without NaCl in the solution).

The buckets were monitored for 52 days. Starting 7 days after addition of *D. dentifera*, we sampled each bucket every 5 days to quantify population densities. On sampling days, we stirred each bucket vigorously, removed a 1L sample, and passed the sample through 153- μm mesh to concentrate the *D. dentifera*. We counted all individuals under a dissecting microscope

and then discarded them. After sampling, we added 1 l of fresh media with the appropriate salt concentration to each bucket. Every 5–6 days, we also removed a 10 ml sample from 10 cm below the surface of the water from each replicate and quantified chlorophyll levels with a fluorometer (described above). We supplemented nutrients twice a week by adding solutions of NaNO_3 and Na_2HPO_4 to maintain a 25:1 mass ratio of N:P, assuming 5% exponential loss per day. We also supplemented food levels by adding 2.0×10^7 cells of *A. falcatus* twice a week (adding 1.3×10^3 cells ml^{-1}) and stirred buckets every 1–2 days to re-suspend algae.

We calculated area under the curve of population densities and chlorophyll levels over time using the trapezoidal rule. The trapezoidal rule estimates the area under a curve (e.g., the population density by time curve) by converting each time step into a trapezoid. The result is that our data are converted to integrate population density and integrated chlorophyll levels, with one value for each replicate. This conversion allows us to correct for differences in timing of population growth within a treatment. The units of this integrated metric are the units of the x-axis variable times the units of the y-axis variable (e.g., individual*days for the area under the *D. dentifera* density curve). We also calculated the peak *D. dentifera* density and the date of peak *D. dentifera* density for each replicate. We compared integrated population density, peak population density, and integrated chlorophyll levels between salt treatments using Student's t-tests. Because our data for the date of peak population density were not normally distributed, we compared date of peak density between salt treatments using a Mann–Whitney *U* test.

Results

In our individual-level experiments, salt treatment did not affect instantaneous birth rate (*b*), instantaneous per capita population growth rate (*r*), or death rates (*d*; $P > 0.05$ for all; Fig. 1). Additionally, body size was not significantly affected by salinity or genotype ($P > 0.05$ for all). Feeding rates were affected by genotype, but not salinity (genotype: $F_{4,76} = 4.45$, $P = 0.003$; salinity: $F_{1,76} = 0.35$, $P = 0.556$). We also found a significant genotype x salinity interaction on feeding rates ($F_{4,76} = 3.66$, $P = 0.009$; Fig. 2;

Table S2). A Tukey's HSD test to investigate this interaction revealed that feeding rates were only affected by salinity in one genotype; the G-4 genotype had lower feeding rates in the high salt treatment compared to the control treatment (Fig. 2).

In the population-level experiment, integrated population densities and peak densities of *D. dentifera* were significantly lower in high salt treatment compared to the control treatment (integrated density: $t(16) = 2.69$, $P = 0.016$; peak density: $t(16) = 2.24$, $P = 0.039$; Figs. 3a, b, 4a). There was a trend for the date of peak *D. dentifera* density to be earlier in the high salt treatments compared to the control treatments, but this was marginally significant ($P = 0.051$; Fig. 4a). Integrated chlorophyll levels were highly variable and unaffected by treatment ($t(16) = 0.60$, $P = 0.560$; Figs. 3c, 4b).

Discussion

We found that increased salinity, equivalent to levels found in freshwater lakes with a history of salinization, decreased time-integrated population densities of *D. dentifera*. In the population-level experiment, integrated densities of *D. dentifera* in our control treatments were almost double those found in the high salt treatments (Fig. 3a). Since *D. dentifera* are dominant consumers of algae and detritus in stratified lakes, the effects of salinization could therefore affect the numerous organisms that interact with this species in natural systems. Additionally, since increased salinity can have direct effects on many other freshwater organisms (Morgan & Iwama, 1991; Cheng & Chen, 2000; Sarma et al., 2006), salinization is likely to have effects on both populations and community interactions in freshwater systems.

Our population-level experiment showed reduced population densities of *D. dentifera* in the high salt treatment, when populations consist of a mixture of genotypes. However, we observed few effects of the same salinity level on individuals. We did observe an effect of salinity on individual feeding rates, but only in one genotype (G-4; Fig. 2). This result indicates that the negative effects of salinity on individual *D. dentifera* can vary with genotype. However, because we only observed an effect of salt treatment on one of five genotypes, feeding rates for the majority of *D. dentifera* genotypes tested were unaffected by treatment. Future

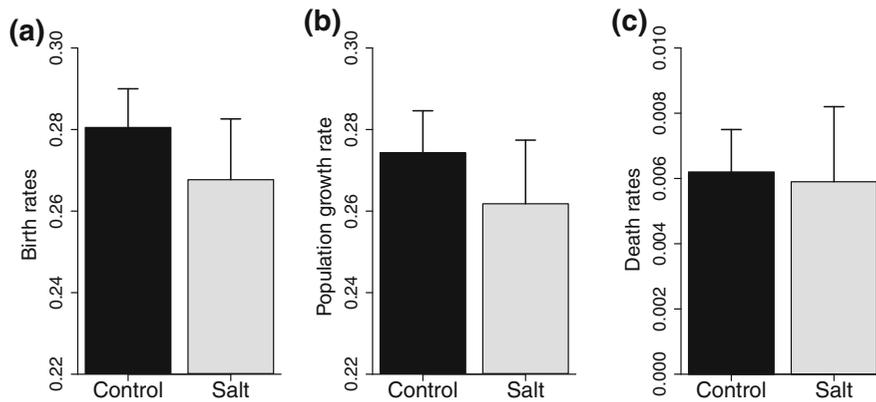


Fig. 1 Average birth and death rates in the control versus high salt (“salt”) treatments (\pm SE). High salt treatments contained an additional 0.6 g l^{-1} NaCl compared to the control treatments. We show **a** birth rates, **b** per capita population growth rate, and

c death rates per day, averaged across five *Daphnia dentifera* genotypes. Each genotype \times treatment combination was replicated 15 times

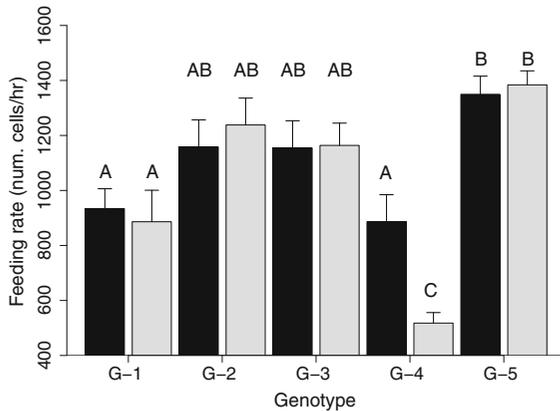


Fig. 2 Average feeding rates across genotypes and salt treatments (\pm SE, $n = 10$). Dark bars represent control treatments while light bars represent high salt treatments. The high salt treatments had an additional 0.6 g l^{-1} NaCl compared to the control treatments. Bars that share a letter are not significantly different from each other

experiments testing more genotypes are necessary to determine if the G-4 genotype is unusual in its response to the increased salinity. Our other individual-level experiments did not detect any effect of salinity on birth or death rates, which are expected to predict potential population growth rates. While a number of previous studies have detected effects of increased salinity on *Daphnia* at the individual level (Arnér & Koivisto, 1993; Martínez-Jerónimo & Martínez-Jerónimo, 2007), these studies used higher salinity levels than our experiments (up to 8500 and $12,720 \mu\text{S cm}^{-1}$, respectively, vs. $1583 \mu\text{S cm}^{-1}$ in this study), likely because

the species tested in these previous studies can be found in brackish waters (*D. magna*). Thus, the lack of effect of salinity in our individual-level experiments may have occurred because our salinity levels were low relative to these previous studies. However, despite detecting few effects on individuals, we found that *D. dentifera* densities were lower in the high salt treatments in the population-level experiment. These results indicate that experiments conducted at the individual level may underestimate the impacts of salinization on *Daphnia*.

Why did results from our individual versus population-level experiments differ? A number of factors inherent to experimental scale may have driven these differences. For example, *D. dentifera* were kept in small volumes of water (10–30 ml) in the individual experiments, but were in large volumes for the population-level experiment (15L). *Daphnia* alter their swimming behavior in response to container size (Dodson et al., 1997) which could influence their feeding rates, and subsequently birth and death rates. Additionally, *D. dentifera* in the individual-level experiments were kept individually and fed ample food, so there was no opportunity for crowding or competition. Brown & Yan (2015) demonstrate that low levels of food can increase the lethal effects of chloride on *Daphnia*. Since we fed *D. dentifera* ample food in the individual-level experiments, any variation in food levels among genotypes and treatments would have been at a level above saturation, and therefore should not have differentially affected the treatments. However, it is very likely that food limitation played a

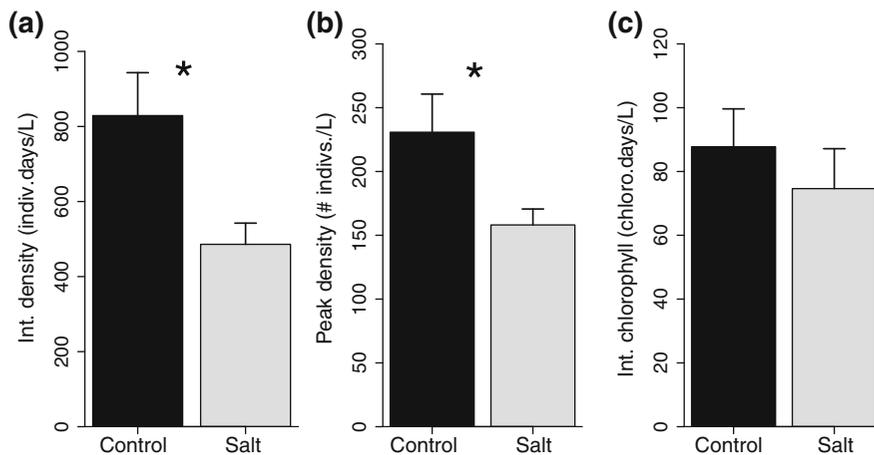


Fig. 3 Average population densities and chlorophyll levels from the population-level experiment in the control versus high salt (“salt”) treatments (\pm SE, $n = 9$, each bucket is one replicate). High salt treatments contained an additional 0.6 g l^{-1}

NaCl compared to the control treatments. We show **a** integrated density of *Daphnia dentifera*, **b** peak density of *D. dentifera* and **c** integrated chlorophyll levels. Significant differences between control and high salt treatments are indicated with a star

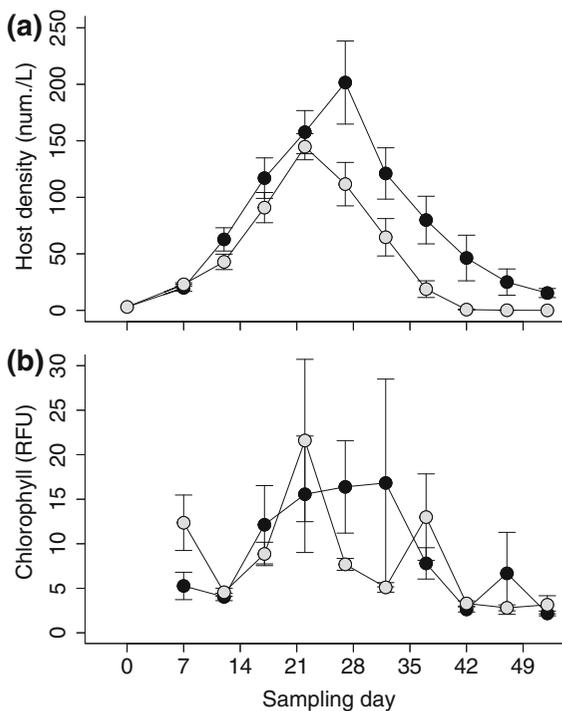


Fig. 4 Population densities and chlorophyll levels through time from the population-level experiment. We show **a** average population densities and **b** average chlorophyll levels in raw fluorescence units (RFU). Dark points indicate control treatments and light points indicate high salt treatments (\pm SE, $n = 9$, each bucket is one replicate). High salt treatments contained an additional 0.6 g l^{-1} NaCl compared to the control treatments

role in limiting *D. dentifera* populations in the population-level experiment because population densities were much higher in the buckets compared to the individual-level experiments (average peak density in the buckets was >150 individuals l^{-1} for both treatments, versus 33 individuals l^{-1} in the individual-level experiments; Fig. 3b). Thus, competition for resources could have increased stress for the *D. dentifera* in the buckets and allowed salinity to have a greater effect on their physiology and behavior. Thus, differences between experimental scales may influence experimental outcome (Skelly, 2002) and effects on individuals may not accurately predict effects on populations.

Interestingly, there was no significant difference in integrated chlorophyll levels between the two treatments (Figs. 3c, 4b). Previous studies have found that increased salt concentrations can reduce photosynthesis rates of freshwater algae (Cook & Francoeur, 2013), which could have directly reduced algal levels in our high salt treatments. However, *Daphnia* densities were lower in the high salt treatment, which should have reduced grazing pressure, indirectly leading to an increase in algal concentrations. Thus, it is possible that the lack of a significant effect of salt on algae in our population-level experiment may reflect the joint direct (negative) and indirect (positive) effects of salt on algae.

Understanding the effects of salinization on freshwater organisms is essential as anthropogenic changes continue to increase freshwater salinity. We found that increased salinity, at concentrations that can be found in natural systems, can reduce population sizes of the common freshwater zooplankton, *D. dentifera*. Additionally, these effects were not predicted from individual-level experiments, indicating that experiments on individuals may underestimate ecologically relevant changes to populations and communities. Thus, understanding the effects of increased salinity on freshwater systems requires knowledge of how salinity affects both individuals and populations.

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