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Journal

ISSN

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et al.

Publication Date

DOI

Peer reviewed

LETTER

Cascading effects of freshwater salinization on plankton communities in the Sierra Nevada

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Scientific Significance Statement

Salinization is a widespread threat to freshwaters globally; however, most studies documenting the effects of salinization on aquatic organisms have taken place in the northeastern U.S.A., Europe, and Canada. Little is known about the effects of road salts in other regions where salt toxicity may be modulated by local water chemistry and local adaptation. We examined the response of plankton from a high elevation Californian lake to NaCl addition. Contrary to previous work, we found an increase in zooplankton biomass and a decline in phytoplankton at concentrations relevant to road salt use. These results indicate salt limitation of zooplankton biomass in highly oligotrophic alpine lakes suggesting salinization via road salt application may lead to steeper biomass pyramids with more zooplankton and lower phytoplankton biomass.

Abstract

Runoff containing road salt (sodium chloride, NaCl) causes the salinization of inland freshwaters, with potentially severe impacts on aquatic species. We performed a mesocosm experiment to test the effects of salinization on plankton community structure in an oligotrophic mountain lake with a limited history of elevated salt concentrations. We exposed plankton communities to a gradient of 30 salt concentrations ranging from 1 to 2900 Cl^- mg L^{-1} for 6 weeks. Adding salt increased zooplankton biomass at concentrations < 500 mg Cl^- L^{-1} while reducing phytoplankton biomass. Zooplankton biomass declined precipitously at higher concentrations, with phytoplankton biomass showing a mirror image increase. The initial increase in zooplankton biomass with salt addition suggests that zooplankton are salt-limited at low ionic concentrations. Additionally, the inverse response of zooplankton and phytoplankton suggests that salinity mainly affects phytoplankton biomass via changes in top-down regulation by grazers.

The widespread use of road salt (NaCl) causes freshwater salinization, threatening aquatic ecosystem integrity (Berger et al. 2019; Hintz and Relyea 2019). Road salts may enter freshwater environments via overland flow paths or build up in soils and groundwater. Much research on salinization has focused on lotic systems; however, lakes may be impacted by salt at as little as 1% impervious catchment land cover, owing to their long water residence times (Dugan et al. 2017), with concentrations expected to increase with urbanization (Corsi et al. 2010; Hintz and Relyea 2019). US EPA guidelines suggest salt concentrations above 230 and 860 mg Cl^- L^{-1} impair biological functions in aquatic organisms under chronic and acute exposure, respectively (US EPA 1988). Thus, increasing chloride concentrations in freshwater systems threaten ecosystem health through changes to biological communities.

Salinization may substantially change the abundance and diversity of aquatic organisms, altering trophic structure through lethal (e.g., osmotic pressure) or sublethal effects (e.g., reduced reproduction or slow growth) (Hintz et al. 2019). However, at low concentrations, salt may be beneficial to organisms; for example, herbivores are often salt-limited as plants store little salt in their cells (Kaspari 2020). As such, zooplankton may retain salt from the environment to maintain the osmolyte content of their hemolymph. As environmental salinity approaches that of the hemolymph, the energetic cost of maintaining osmotic balance should be reduced. However, freshwater zooplankton are unable to maintain intracellular solute concentrations below that of their environment (hyperosmotic regulators). Therefore, as salt concentrations rise beyond that of the hemolymph, ion uptake should increase alongside energy expenditure until too much water is lost from cells and normal function ceases (Hart et al. 1991). The limit at which cellular functioning ceases varies significantly within and among species (Hintz et al. 2019). Consequently, communities with a larger proportion of tolerant species or genotypes are more resistant to change as salt concentrations increase. Further, salinization may change ecosystem functioning through direct or indirect effects on decomposition and nutrient cycling, thus compromising vital ecosystem services (Berger et al. 2019). Determining the impacts of salt on aquatic communities is, therefore, crucial for the implementation of strategies to manage salt runoff into freshwater habitats.

Biotic responses to salinization are taxonomically and geographically heterogeneous. Smaller animals (e.g., zooplankton) are more sensitive to salt than larger organisms (e.g., fish), but responses differ substantially among species (US EPA 1988; Castillo et al. 2018). For zooplankton, an increase in salinity has been linked to a reduction in species richness (Jeppesen et al. 2007; Lin et al. 2017). For example, as salinity increases in brackish lagoons, cladocerans, which play a crucial role in regulating phytoplankton, are often lost, and communities become dominated by copepod and rotifer species (Jeppesen et al. 2007 and references therein). Further, shifts in zooplankton biomass with increased salinity often follow nonlinear patterns, with substantial variability in salt tolerance thresholds within and among species (Jeppesen et al. 2007; Corsi et al. 2010; Hintz et al. 2019). Factors such as exposure history and regional connectivity may decrease salt sensitivity through adaptive change or increased diversity (Thompson and Shurin 2012; Coldsnow et al. 2017; Hintz et al. 2019). Further, salt toxicity may be modulated by water chemistry; for example, studies have found that freshwater zooplankton are more sensitive to salt when calcium concentrations are low (Elphick et al. 2011; Arnott et al. 2020). As such, it is important that local and regional factors are considered in studies assessing the impacts of road salt. Studies investigating the effects of salinization on freshwater ecosystems are concentrated in cold regions, such as Canada and the northeastern U.S.A. (Palmer and Yan 2013; Hintz and Relyea 2017, 2019),

with a limited understanding of how salinization may influence freshwater biota in other regions. Given the widespread extent of freshwater salinization (Dugan et al. 2017) and the variability in species responses, there is a need to understand location- and species-specific responses to salinization using a robust gradient design to detect nonlinear responses.

Here, we used a pond mesocosm experiment to test the effect of salinization on community biomass, species composition, trophic level abundance, and size structure of a natural plankton assemblage from an oligotrophic alpine lake (Convict Lake) in the Eastern Sierra Nevada of California. Roads in the Eastern Sierra have been treated with a salt-brine solution since 2014, but there is little understanding of how this may affect the freshwaters in the region, which supplies 60% of California's drinking water (Harootunian 2018). While the Eastern Sierra has a long history of salinization research due to Mono Lake and other naturally hypersaline lakes (Dana and Lenz 1986), no studies have focused on the impact of salinization on dilute high elevation lakes. We expected increased salinity to reduce zooplankton biomass and increase the abundance of smaller, more salt-tolerant rotifers. We also expected that the response of zooplankton would propagate to phytoplankton due to top-down control.

Methods and materials

Background

Convict Lake, in the Sierra Nevada (CA), sits at an elevation of 2393 m, has a maximum water depth of 43 m and a surface area of 0.68 km^2, and is presently used for recreational fishing (*Oncorhynchus mykiss* and *Salmo trutta*). Convict Lake is oligotrophic and at the time of our experiment nutrient levels were low (Total Nitrogen = 0.12 mg L^{-1}, Total Phosphorus = below detection, < 0.05 μg L^{-1}), chloride (Cl$^-$) concentrations were < 2 mg L^{-1}, and calcium (Ca) concentrations were 26.3 mg L^{-1}.

Experiment

We conducted a mesocosm experiment using a gradient design to understand the effect of NaCl on plankton communities. We established 30 mesocosms (1000 L, round tubs, 183 cm diameter, and 61 cm tall) at the Sierra Nevada Aquatic Research Lab (SNARL) into which we added water from Convict Creek, which drains from Convict Lake. We installed temperature loggers into five randomly chosen mesocosms (HOBO® pendant, Onset, Massachusetts, U.S.A.) and added zooplankton after 3 d. We collected zooplankton from Convict Lake by filtering a volume of water equivalent to the total volume of the mesocosms using vertical tows from 30 m with a 64 μm mesh net. Zooplankton were mixed in a large container with lake water, and equal aliquots were added to each mesocosm. We covered the mesocosms with 60% shade cloth to prevent aerial colonization of invertebrates and allochthonous inputs. We added 0.0035 mg P L^{-1} in the form of K$_2$HPO$_4$ and 0.196 mg N L^{-1} in the form of NH$_4$NO$_3$ to

supply nutrients lost to periphyton growth. The day after zooplankton were added, we mixed NaCl (Chem-Impex International Brand, 99.8% pure) into mesocosms at 30 concentrations, and at week 6 these concentrations ranged from 1.2 to 2920 mg Cl^- L^{-1} (Fig. 1). Chloride concentrations were chosen to incorporate ecologically relevant concentrations (100s to 1000s Cl^- L^{-1}, Dugan et al. 2017) and to exceed plankton biological thresholds to ensure any nonlinearities in responses were captured. We predicted chloride concentrations at week 0 based on the relationship between chloride and conductivity at week 6. Chloride concentrations increased from week 0 to 6 due to evaporation in mesocosms. There was no salt addition at the lowest concentration (week 6: 1.2 mg Cl^- L^{-1}), which was our control treatment. We used a gradient experimental design because we were interested in revealing the potentially nonlinear effects of salinization on

freshwater zooplankton and identifying any thresholds in their response (Kreyling et al. 2018).

Sampling

We sampled the mesocosms once before salt addition on day 0 (12 July 2018; 0 week), and after salt addition on days 21 (3 weeks) and 42 (6 weeks). We measured conductivity, dissolved oxygen, and pH using a handheld meter (YSI Professional Plus) at each sampling point. At the final time-point (week 6), we took a 50 μm filtered water sample from each mesocosm and measured Cl^- using an ion chromatograph (Dionex ICS-2000 Ion Chromatograph).

To sample zooplankton, we collected water using a depth-integrated tube sampler for a total sample volume of 2% of the mesocosm on weeks 0 and 3, and 10% on week 6. We filtered samples through a 50 μm sieve and preserved them in 70% ethanol. We counted zooplankton in aliquots until at least 200 individuals (adults and juveniles) per sample were identified to the lowest practical taxonomic resolution at ×80 magnification. In each sample, we photographed 15 individuals of each species and measured their body length. We calculated zooplankton biomass for each species using published weight-length regressions (Bottrell et al. 1976; Rosen 1981).

We sampled chlorophyll-*a* (Chl *a*) (proxy for phytoplankton biomass) by filtering 200–500 mL of water through a 0.45 μm glass fiber filter (Whatman GF/F). We immediately froze filters and analyzed Chl *a* no longer than 1 month after collection by extraction in 20 mL of 90% acetone for 24 h at 4°C. We measured Chl *a* using a Trilogy Laboratory Fluorometer (TurnerDesigns, San Jose, California, U.S.A.).

Statistical analyses

Our analyses focus on trends at our final time-point, week 6, after sufficient time for salt to affect zooplankton and phytoplankton communities (Supporting Information Fig. S1). To determine if body size shifted across all species in our experiment, we calculated community abundance weighted mean body size. To understand the influence of chloride on zooplankton biomass, Chl *a*, mean body size, and species abundances, we use a thin-spline generalized additive model (GAM) with 10 knots and a smoothing parameter of 0.6. We chose to use a GAM because it does not assume linearity between variables; thus, we report the estimated degrees of freedom (edf) and *p* values of the model's smooth term. As there were no noticeable nonlinear patterns in body size across the three dominant taxa in our experiment, we used linear regression to determine the relationship between species average body size and chloride. Body size change may occur if increasing salinity alters zooplankton community composition, favoring smaller-bodied individuals or via intraspecific shifts in size due to sublethal effects (e.g., reduced growth). To estimate top-down control of zooplankton, we calculated zooplankton filtering rate based on zooplankton biomass for both cladocerans and all other zooplankton and
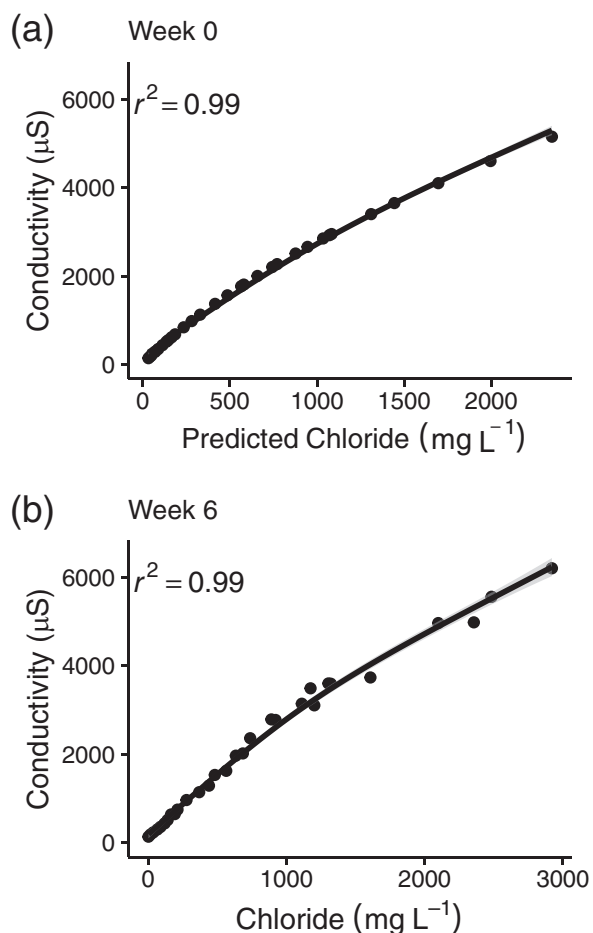

Fig 1. Relationship between chloride concentration and conductivity at (**a**) week 0, and (**b**) week 6. Chloride concentrations were predicted based on the model in plot (**b**), as chloride was only measured at week 6. Data are fitted with second-order polynomial models and have 95% confidence intervals shown in gray (*n* = 30).

in each mesocosm from equations 2 and 4 in Peters and Downing (1984).

We used one-way ANOVA to determine if the average temperature was different among mesocosms with temperature loggers ($n = 5$) and to understand if chloride affected pH. We measured temperature and pH to ensure that starting conditions were similar. All statistical analyses were performed using R version 3.6.2 and using the R packages "mgcv" v. 1.8-21 and "lme4" v 1.1.17 (Wood 2011; Bates et al. 2015).

Results

Zooplankton biomass increased with greater salinity at Cl^- concentrations up to 481 mg Cl^- L^{-1}, possibly indicating salt-limitation at low salinities. Above this concentration, zooplankton biomass declined, reaching zero zooplankton at 2097 mg Cl^- L^{-1} (GAM; edf = 2.349, r^2 = 0.312, $p < 0.0005$, Fig. 2, Supporting Information Table S1). Estimated zooplankton filtering rate remained at a similar level ($\sim$ 6 mL d^{-1}) until $\sim$ 1320 mg Cl^- L^{-1}, before sharply declining, indicating top-down control remained strong at low-moderate salt concentrations (GAM; edf = 2.834, $p < 0.0001$, r^2 = 0.734, Supporting Information Fig. S2). The average zooplankton body size in the community declined with increasing chloride concentration (GAM; edf = 2.091, $p = 0.0007$, r^2 = 0.279; Supporting Information Fig. S3). The body size decline was partially driven by shifts in community composition as only small-bodied Ostracods were present at the highest salinities. Within our three dominant species, trends in body size were idiosyncratic, where the average body size of *Eucyclops agilis* increased, *Chydorus sphaericus* decreased, and there was no change in *Daphnia pulicaria* body size with salinity (Supporting Information Fig. S3). We found a total of six species across all treatments at week 6; however, the maximum species richness in any mesocosm was five. As salinity increased, species richness declined. Above 191 mg Cl^- L^{-1} and 890 mg Cl^- L^{-1} *Leptodiaptomus signicauda* and nauplii were respectively absent from mesocosms (Fig. 3). At concentrations between 211 and 1200 mg Cl^- L^{-1}, mesocosms were primarily composed of *D. pulicaria*, *E. agilis*, and *C. sphaericus*. At salinities over 1200 mg Cl^- L^{-1}, ostracods were present in the mesocosms, though at very low abundances and only in 4 of 30 samples.

Trends in phytoplankton Chl a concentrations mirrored those in zooplankton, indicating top-down control. Phytoplankton biomass declined at greater salinity levels up to 500 mg Cl^- L^{-1} and remained at this level to $\sim$ 900 mg Cl^- L^{-1}, above which phytoplankton biomass increased with Cl^- concentrations to 2355 mg Cl^- L^{-1} (GAM; edf = 1.528, $p < 0.0001$, r^2 = 0.620; Fig. 2, Supporting Information Table S1). Mean water temperatures across mesocosms with loggers ranged from 20.1°C ($\pm$ 3.3 SD) to 20.7°C ($\pm$ 3.6 SD) over the entire experimental period ($n = 539$, measured every 2 h for 6 weeks). There were no differences in
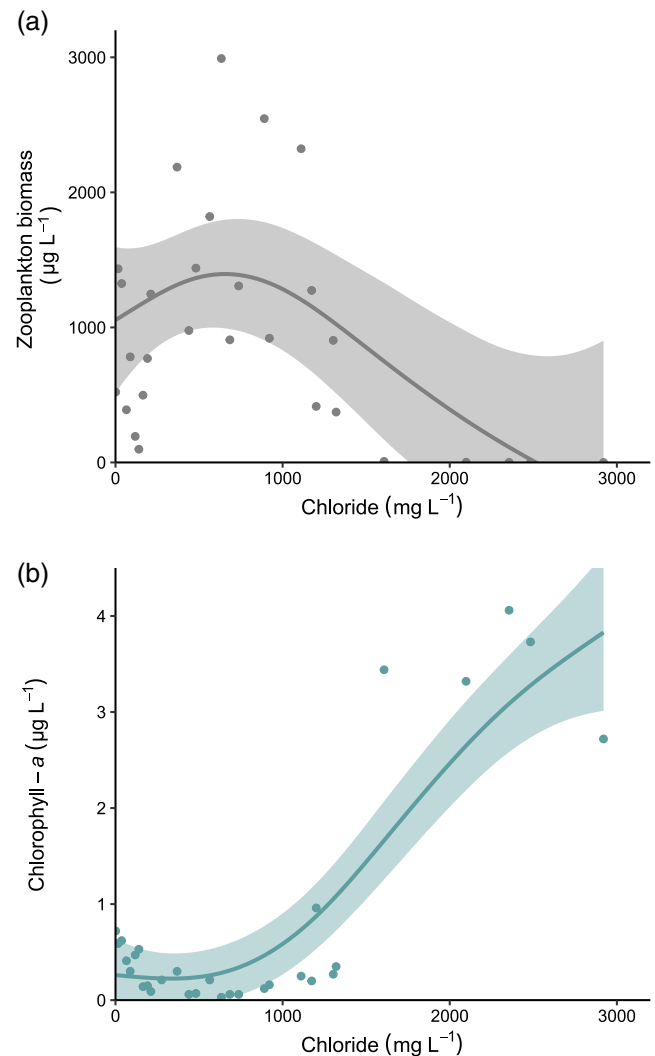

Fig 2. Effect of salt, as chloride, on (**a**) zooplankton and (**b**) phytoplankton biomass after 6 weeks. Data are fitted with a thin spline GAM with a 95% confidence interval ($n = 30$).

average water temperatures across the mesocosm array ($F_{1,3} = 0.026$, $p = 0.883$). We found an increase in pH with chloride concentration (pH ranged from 7.8 to 8.4), though two high pH measurements leveraged this relationship at the upper end of the Cl^- gradient ($F_{1,28} = 6.665$, $p = 0.0154$; Supporting Information Fig. S4).

Discussion

Plankton abundance and biomass varied nonlinearly with salinization, leading to shifts in trophic structure. Surprisingly, zooplankton biomass responded positively to salt addition at levels relevant to road salt application suggesting that the ambient low-salinity conditions in alpine lakes induce osmotic stress in zooplankton such that salt is a limiting
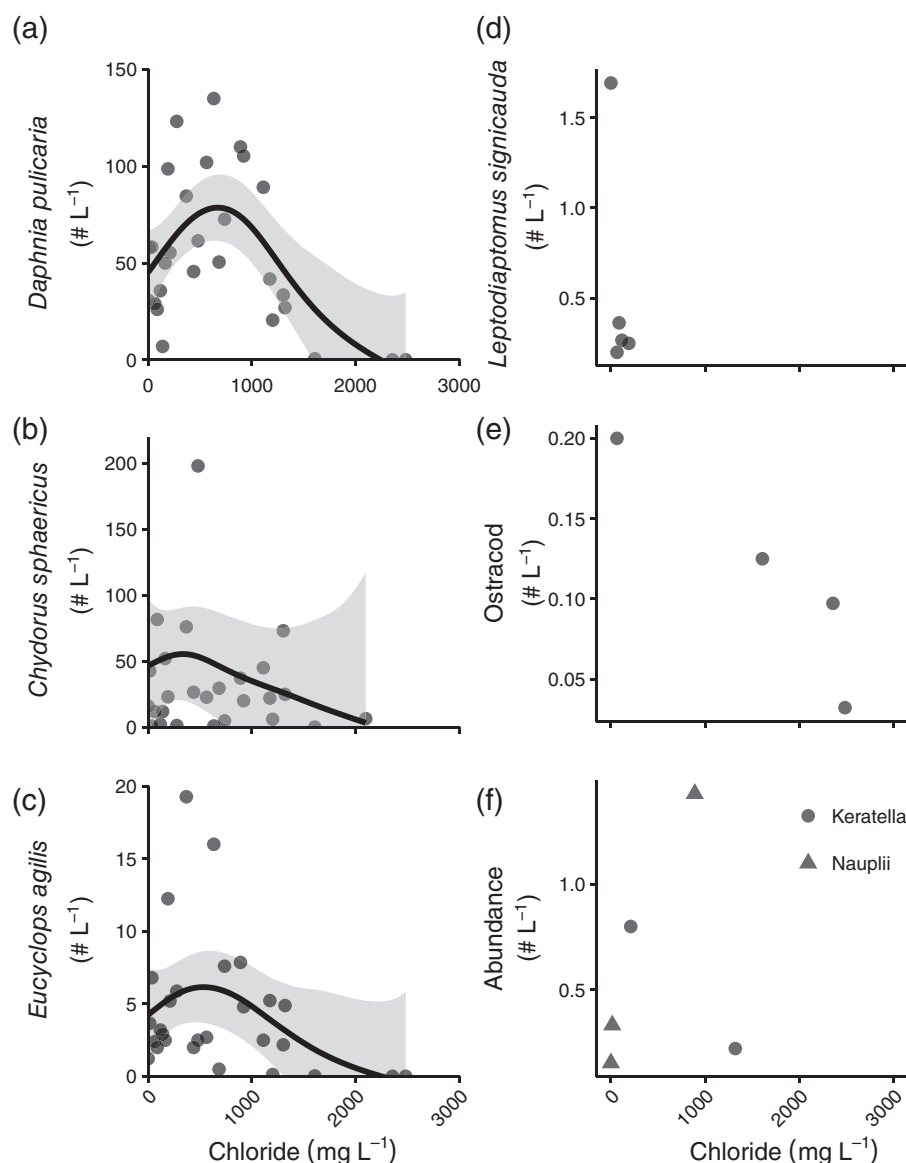
Fig 3. Shifts in species abundance with increasing salt concentration, where species abundance is zero these data are not shown (**a-e**). Abundance plots with > 5 data points are fitted with a thin spline general additive model with a 95% confidence interval in gray (model details in Supporting Information Table S1). In plot (**f**), both *Keratella* and nauplii are shown due to their low frequency.

factor to secondary production. While studies often report a reduction in zooplankton biomass with increasing salinity (Thompson and Shurin 2012; Searle et al. 2016; Hintz et al. 2017), our data suggest salt limitation of zooplankton growth at ambient salt concentrations. Above a threshold of around 500 mg Cl$^-$ L^{-1}, zooplankton declined precipitously while phytoplankton increased in proportion. Further, our data indicate that zooplankton as a group are more sensitive to salinization than phytoplankton, which respond mainly via the indirect, top-down effects of zooplankton grazing. Trophic structure of alpine aquatic ecosystems may, therefore, show a nonlinear response to salt addition, with steeper biomass pyramids (more consumer biomass relative to producers) at low levels, and a reversal to phytoplankton dominated system above a critical threshold level of salinity.

Zooplankton

Our data suggest that the energetic cost of osmoregulation limits secondary production at low ionic concentrations, as zooplankton biomass increased above that of the lowest salt concentrations up to ∼ 500 mg Cl$^-$ L^{-1} (Fig. 2). Other studies have found that zooplankton abundance is reduced at salinities ranging from 200 to 800 mg Cl$^-$ L^{-1} (Searle et al. 2016; Hintz et al. 2017; Sinclair and Arnott 2018). Thus, in contrast to other studies, our data suggest salt limitation of

zooplankton biomass at ambient salt concentrations in highly dilute waterbodies (Kaspari 2020). Such salt limitation may have broad consequences for waterbodies where water abstraction, drought, or sea-level rise results in elevated salt concentrations (Jeppesen et al. 2015). For example, in past studies, large-bodied grazer species (e.g., *Daphnia* spp.) are lost in favor of more salt-tolerant and smaller-bodied species (e.g., rotifers) with increasing salinity potentially weakening top-down control (Thompson and Shurin 2012; Coldsnow and Relyea 2018). However, where individuals are salt-limited, top-down control may be retained or enhanced with salinization.

Though salinization reduced species richness in our experiment, our increase in zooplankton biomass was not driven by competitive release from *Daphnia* as found in other studies on road salts and from brackish waters (e.g., Jeppesen et al. 2007; Van Meter and Swan 2014; Lin et al. 2017). At salt concentrations above 500 mg Cl^- L^{-1}, a copepod (*E. agilis*), and two cladoceran species (*D. pulicaria, C. sphaericus*) were dominant while a copepod species (*L. signicauda*) and nauplii declined. Across all species, there was a reduction in abundance-weighted average body size with increased salinity, though this trend was heavily influenced by the presence of small-bodied ostracods at high salinities and the disappearance of all other taxa. As such, our data demonstrate that a reduction in zooplankton species richness and changing abundance with increased salinity is most important for generating the change in trophic level biomass, rather than shifts in overall body size. However, shifts in body size may be more pronounced in systems with a top predator (fish, predatory macroinvertebrates). For example, in tri-trophic systems, top-down control by fish may reduce the density and the body-size size of zooplankton communities via size-selective predation (Jakobsen et al. 2004; Lin et al. 2017; Gutierrez et al. 2018). Further, the presence of predators may increase zooplankton richness, as large-bodied cladocerans become less abundant at salt concentrations lower than predicted by salt toxicity alone, allowing a more diverse community to establish (Jensen et al. 2010). As such, to understand the effects of salinity on biomass pyramids, both biological (predation) and physiological (toxicity) effects need to be accounted for in future studies.

Phytoplankton

Phytoplankton biomass covaried negatively with zooplankton biomass and zooplankton filtering rate, consistent with top-down control (Fig. 2; Supporting Information Fig. S2). The loss of grazing species, such as cladocerans, often leads to increases in phytoplankton, which may compromise ecosystem services (e.g., reduction in water quality) (Van Meter and Swan 2014; Hintz et al. 2017). As zooplankton were initially enhanced by salt addition, our data show a concordant reduction in phytoplankton relative to the control to 500 mg Cl^- L^{-1}, beyond which phytoplankton biomass rapidly increased. Our data suggest that phytoplankton as a

group tolerate a broad range of salinity in our ecosystem, although the composition of the community very likely changed across the wide range of salinity in our experiment. The dominant algal species were single-celled green algae, which precluded visual identification; however, future studies may benefit from examining shifts in phytoplankton composition using other techniques. Here, phytoplankton most likely responded to salinity indirectly via its effects on zooplankton. Phytoplankton were released from grazing in our system due to the loss of zooplankton at chloride concentrations over 1300 mg Cl^- L^{-1} (Supporting Information Fig. S2). Therefore, lake zooplankton and phytoplankton showed a nonlinear response to salinity with steeper biomass pyramids under low levels of salinization and a sharp threshold reversal at intermediate concentrations.

Mechanisms

Variation in responses to salinization by plankton have been linked to predation, disturbance, adaptation, dispersal, and water chemistry (Waterkeyn et al. 2011; Thompson and Shurin 2012; Coldsnow et al. 2017; Hintz and Relyea 2017). While the mechanisms behind the relatively high salt tolerance of zooplankton here are unknown, mediation of salt toxicity by the relatively high calcium concentrations in our study lake is a plausible explanation. For example, Canadian Shield lakes have 9× lower average calcium concentrations than our study lake (2.8 ± 3.8 mg Ca L^{-1} and 26.3 mg Ca L^{-1}, respectively) (Palmer and Yan 2013). Low calcium concentrations (< 1.5 mg Ca L^{-1}) may limit zooplankton growth rates, delay maturation, and reduce brood size (Ashforth and Yan 2008; Arnott et al. 2017; Arnott et al. 2020), and high calcium concentrations have been associated with increased *Daphnia* salt tolerance, as calcium decreases cell membrane permeability (Elphick et al. 2011). As such, high calcium concentrations or a combination of high calcium and other factors (e.g., pH) may have contributed toward the increase in zooplankton biomass with increasing salinity at low salt concentrations.

The regional context may also be an important factor in determining zooplankton salt tolerance. Dispersal from nearby waterbodies may rapidly moderate zooplankton responses to salinity (e.g., in 2.5 months; Coldsnow et al. 2017; Hintz et al. 2019). However, our study lake is not saline, and contains few species known to tolerate a broad range of salinities (Hammer and Forró 1992; Lee and Petersen 2002). Nevertheless, the regional context may play a role in maintaining salt-tolerant genotypes via dispersal from nearby saline lakes in the region (e.g., Mono Lake, Owen's Lake) (Sinclair and Arnott 2018). Regional context can influence stressor tolerance even in undisturbed locations; for example, copepods originating from lakes with no history of acidification have a greater acid tolerance when embedded in acid-dominated landscapes than circumneutral landscapes (Negrín Dastis and Derry 2016). Regardless of the mechanism,

the increase in zooplankton biomass with increasing salinity indicates a novel interaction between salinity and fitness in our zooplankton community with potential strong top-down consequences for phytoplankton.

Conclusions

Increasing chloride concentrations in freshwater systems have led to concerns about impaired ecosystem health, drinking water quality, and fisheries productivity; however, very little is known about the effects of salinization on lakes compared to other contemporary stressors (e.g., acidification, nutrients). Our data are the first to explore how salinization may affect a natural plankton community from a high-elevation freshwater lake community in the Sierra Nevada mountain range. We show that zooplankton biomass was enhanced at salt concentrations relevant to road salt addition, indicating that zooplankton may be salt-limited at ambient low ionic concentrations in our study system. Further, our data suggest that communities in the Eastern Sierra region have a higher tolerance to salinization than in other geographic contexts (e.g., Canada, northeastern U.S.A., Europe), which may be associated with the high calcium concentration of our study lake. In contrast, phytoplankton were mainly affected by salinity via top-down changes in zooplankton. Therefore, consideration of local water chemistry and traits of the local and regional species assemblage is important for predictions of the ecological effects of road salt inputs.

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