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Dispersal as a Buffer Against Zooplankton Community Change in Response to Fluctuating Salinity Levels on the Great Plains

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Dispersal as a Buffer Against Zooplankton Community Change in Response to Fluctuating Salinity Levels on the Great Plains

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Abstract

The North American Great Plains is home to thousands of closed-basin lakes that are sensitive to changes in hydrology. Climate change models predict increased aridity in this region over the coming century, which is expected to lead to higher salinity levels in many freshwater lakes. Increases in salinity levels may impact zooplankton communities, as laboratory experiments show that many freshwater species have a low tolerance for elevated salinity levels, and field data demonstrate that salinity is the primary factor structuring aquatic communities on the Great Plains. Changes to zooplankton communities could lead to a trophic cascade based on their important position in the lower food web, making it important to understand how they might respond. Zooplankton in lakes undergoing salinization may exhibit shifts in community structure toward salinity-tolerant species and a decrease in richness, diversity, and abundance. As a counter, the dispersal of zooplankton across the landscape from neighbouring water bodies may be able to compensate for the losses of sensitive zooplankton due to local adaptation to elevated salinities as well as taxonomic and functional redundancies in the regional species pool. For this study, I ran a field experiment at Kenosee Lake in southern Saskatchewan where salinities and zooplankton dispersal rates were artificially manipulated over six weeks. We found that increased salinities led to reduced zooplankton abundances and species richness levels, mainly due to a loss of cladocerans. However, enclosures with moderate salinities that received dispersers maintained a community composition similar to undisturbed control communities. The persistence of cladocerans in moderate salinity enclosures receiving dispersal may have been caused by a source-sink effect or the introduction of salinity-tolerant cladocerans. I ran laboratory toxicity assays using *Daphnia* collected from the plains and found that intraspecific variation in salinity tolerance exists, making the latter explanation plausible. My results indicate that dispersal could play an important role in determining how zooplankton communities respond to increased salinity levels, demonstrating the need to preserve biodiversity in the regional species pool and maintain the vectors and pathways that facilitate the dispersal of zooplankton among lakes on the Great Plains.

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Introduction

1.1. General overview

The North American Great Plains cover a vast expanse of land located east of the Rocky Mountains and west of the Mississippi River (Figure 1.1, 1.2). Variability in moisture regimes across space and time along with the topography of the region have produced diverse aquatic ecosystems that exhibit a range of salinities found in few other places on earth (Williams, 1999; Last & Ginn 2005). In the coming decades, salinity levels in these lakes are expected to increase due to increases in temperature and reductions in precipitation that could prolong periods of drought (Dai, 2013; Michels et al., 2007; Sauchyn et al., 2002). Rising salinity levels could significantly affect the biology of these systems, as past studies of salinized freshwaters show salinity-driven changes in the abundance and richness of phytoplankton, zooplankton, macroinvertebrates, and fish (Piscart et al., 2006; Corsi et al., 2010; Wedderburn et al., 2012; Jeppesen et al., 2015).

The impacts of elevated salinity levels in freshwater ecosystems are complex and can impact different taxonomic groups in a myriad of ways. At the most basic level, elevated salinity levels affect life history parameters such as life span, generation time, and reproductive rates for all major trophic levels including primary producers, microinvertebrates, macroinvertebrates, and fish (Bœuf & Payan, 2001; Martínez-Jerónimo & Martínez-Jerónimo, 2007; Munns & Tester, 2008). Macrophytes can face higher osmoregulatory costs and less nutrient availability (e.g.

phosphorus) when waters are stagnant and deprived of freshwater inputs that help mix sediment (Velasco et al., 2006). For green algae, increases in NaCl can induce the withdrawal of water from vacuoles, causing death when vacuoles are exhausted (Hintz et al., 2017). For certain types of zooplankton, increases in NaCl have been reported to significantly lower average life expectancy, total progeny, clutch size and reproductive rates (Martínez-Jerónimo & Martínez-Jerónimo, 2007). Fish have a more complex relationship with salinity, where the most ideal metabolic costs for growth rates are found in intermediate salinities (Bœuf & Payan, 2001). Salinity can also have synergistic effects with, or direct influence on pH, temperature, and dissolved oxygen, which further complicates how salinity will impact aquatic biota (Velasco et al., 2006).

At acute thresholds, the effects of salinity are directly observable over a short period of time through single or ongoing exposures. Often these effects are measured by the lethal concentration required to cause mortality in 50% of the population (LC50). Lethal toxicity tests conducted on riverine species indicate that microinvertebrates were more sensitive (lower LC50s) to NaCl than macroinvertebrates or fish, but that the latter two groups are more susceptible to indirect salinity effects such as changes to prey abundances (Kefford et al., 2007). According to the EPA (1988), *Daphnia pulex* (a common zooplankton microinvertebrate) was the most chloride-sensitive out of the twelve taxonomically diverse genera studied including trout, eel and snails. These findings suggest that microinvertebrates, such as zooplankton, are more sensitive to salinity changes than organisms at higher trophic levels.

Zooplankton are a group of heterotrophic plankton that play an important role in the aquatic food web, providing a key link between primary producers and larger macroinvertebrates and fish. The structure of zooplankton communities in Great Plains' lakes is primarily controlled by salinity (Wissel et al., 2011). Species diversity declines as salinity increases between 3-50 g L^{-1} until only one or two species are present at the highest salinities. Harpacticoid copepods and *Artemia* tend to dominate high salinity lakes, while low salinity lakes can support species of *Daphnia*, *Ceriodaphnia*, and calanoid copepods (Wissel et al., 2011). Past studies on aquatic ecosystems in other parts of the world have also found that increases in salinity can sharply reduce taxonomic richness, diversity, abundance, and biomass of zooplankton, and can cause shifts in community composition toward halotolerant species (Schallenberg et al., 2003; Wissel et al., 2011; Thompson & Shurin, 2012; Hintz et al., 2017). Although relationships between zooplankton diversity and salinity are clearly established, little research has been conducted to determine survival thresholds for individual species, or to determine how much variability in salinity tolerance might exist within a single species that inhabits lakes spanning a salinity gradient.

An ecological mechanism that could increase the resilience of zooplankton communities to rising salinities is dispersal. The spatial insurance hypothesis suggests that dispersal of individuals among lakes, combined with functional redundancies in a regional species pool, could allow for the replacement of extirpated individuals or species by organisms that fill similar niches (Berg et al., 2010; Loreau et al., 2003). In this case, the dispersal of a salinity-tolerant individuals or species from a nearby lake into a lake experiencing salinity increases could compensate for losses of individuals or species sensitive to increases in salinity (Figure 1.3). The likelihood that spatial insurance would act to counter salinity-driven changes in zooplankton communities requires two assumptions: 1) That dispersal occurs at a temporal and spatial scale significant to compensate for losses; and 2) That variation in salinity tolerance among individuals and species occurs among lakes with varying salinity levels. It is difficult to evaluate the first assumption without field studies in the region of interest, as published studies on zooplankton dispersal differ wildly in their conclusions about dispersal rates (Audet et al., 2013; Cohen & Shurin, 2003; Havel & Shurin, 2004; Jenkins & Underwood, 1998; Jenkins, 1995; Márquez & Kolasa, 2013; Vanschoenwinkel et al., 2008). A few past studies support the second assumption, as there is evidence that zooplankton can evolve to tolerate higher salinity levels (Coldsnow et al., 2017; Latta et al., 2012), and that there are differences in salinity tolerance both within and among species (Kelly et al., 2012; Weider & Hebert, 1987). Published studies provide some support for the spatial insurance hypothesis in the case of rising salinities (Loreau et al., 2003; Thompson & Shurin, 2012; Symons & Arnott, 2013) and for zooplankton communities exposed to several other stressors such as changes to nutrients, connectivity and invasive species (Strecker, 2007; Staddon et al., 2010; Symons & Arnott, 2013).

Climate-driven increases in salinity may have severe consequences for freshwaters in the Great Plains, making it important to examine how these ecosystems will respond. This project incorporates a field mesocosm experiment and laboratory toxicity tests to study the problem. The field portion tested the effects of salinization and the role of dispersal for buffering zooplankton community structure in the face of salinity change. As a supplementary study, intra and inter-specific toxicity experiments were conducted to determine if variation in salinity tolerance among individuals and species occurs among lakes with varying salinity levels. Examining the role of dispersal as a mechanism to buffer against salinity-driven change in zooplankton communities could help improve our understanding of metacommunity theory, and more specifically fill in the gaps needed for current management and future predictions of biotic change in this region.

1.2. Research objectives

Given the importance of salinity for structuring zooplankton communities, it is likely that salinity changes could have significant impacts on zooplankton in Great Plains lakes. However, it is unclear if dispersal of zooplankton among lakes could act to buffer against salinity-driven changes in zooplankton communities. My thesis addressed the following objectives:

1) To determine how zooplankton communities will change in response to increased salinity levels in the Northern Great Plains
    - Salinity will influence community structure, decrease taxonomic richness and diversity, and functional richness and diversity.

2) To assess whether the spatial insurance hypothesis holds true for zooplankton communities responding to salinity increases
    - Dispersal will act to decrease changes in community structure, taxonomic, and functional measures caused by increased salinity.

3) To investigate intraspecific salinity tolerances as a plausible mechanism contributing to spatial insurance effects
    - Members of the same species will have varying salinity tolerances due to local adaptation.

1.3. Zooplankton ecology

Zooplankton are a group of heterotrophic microscopic organisms with a weak swimming ability. They are ubiquitous, inhabiting most freshwater ecosystems on earth, including wetlands, rivers, ponds, and lakes (Suthers & Rissik, 2009). Some members of the zooplankton spend their entire life cycle living in the water column (holoplankton), while others, such as larval insects, only spend parts of their life under water (Suthers & Rissik, 2009). They are a diverse group that fill a variety of niches, with species exhibiting different habitat preferences (e.g. pelagic versus littoral), food preferences (e.g. herbivores versus predators) and feeding strategies (e.g. filtering versus capturing) (Barnett et al., 2007). Zooplankton are generally responsive to environmental changes, making them a key group to examine when trying to understand the impact of stressors.

Many zooplankton are filter-feeding herbivores, grazing on phytoplankton such as filamentous algae or diatoms (Fryer, 1980). In lake ecosystems, *Daphnia* are often the dominant herbivores while calanoid copepods act as primary grazers in marine habitats (Sommer, 2006). Other zooplankton can be omnivorous or carnivorous, feeding on smaller or sometimes even larger animals than themselves (e.g. chironomid larvae, cladocerans). Freshwater cyclopoids are good examples of opportunistic feeders as their group is comprised of herbivorous, carnivorous and omnivorous species with cannibalistic tendencies at times (Fryer, 1980; Sommer, 2006).

Zooplankton are considered an important component of aquatic food webs, as they play a role in transferring energy from primary producers (algae and phytoplankton) to higher trophic consumers. Planktivores are a highly diverse group describing vertebrates and invertebrates that feed on planktonic organisms, including zooplankton. Fish are facultative planktivores in aquatic ecosystems, relying on visual cues to feed on large *Daphnia* when available but otherwise are dependent on non-planktonic foods (Brooks, 1968). Other planktivorous vertebrates include marine mammals, freshwater amphibian larvae and even some shorebirds common to the North American prairies. Invertebrate planktivores include insects, water mites and numerous crustaceans (e.g. decapods, amphipods, gastropods) (Greene, 1985). Zooplankton represent a shared food resource sustaining a multitude of aquatic organisms from larval to adult stages.

Two abundant and well-studied groups of zooplankton are the cladocerans (Order: Cladocera) and copepods (Subclass: Copepoda). Cladocerans are generally short-lived with short generation times in comparison with copepods. Cladocerans in the genus *Daphnia* been shown to have an average lifespan of two months, reproducing every 2-3 days depending on temperature and average adult mass (Gillooly, 2000; Martínez-Jerónimo & Martínez-Jerónimo, 2007). In contrast, *Leptodiaptomus sicilis,* a common calanoid copepod, lives 7 to 12 months often with only a single brooding period (Herzig et al., 1980). When conditions are favourable, cladocerans achieve their short generation times by parthenogenesis, allowing for asexual reproduction without male fertilization. In contrast to cladocerans, copepods require both male and female individuals for sexual reproduction, producing eggs that hatch into a larval stage called a nauplius (LeBlanc et al., 1997). If conditions deteriorate, both cladoceran and copepod populations will produce resting eggs that can hatch when favorable conditions return (Ortells et al., 2005; Witty, 2004)

1.4. Responses to salinity

Salinization could impact zooplankton at a variety of scales from the physiological stress experienced by an individual to the changes in species composition found at the community level. The following section will discuss the potential effects of rising salinity levels at a variety of scales (physiological, intraspecific, interspecific, community) and will then discuss how other abiotic variables may interact with salinity to affect zooplankton.

1.4.1. Physiological effects

Increases in salinity can lead to physiological complications concerning growth and reproduction caused by osmotic stress (Latta et al., 2012). Osmotic stress occurs when the external environment has a higher concentration of salts than inside the cells, leading to a loss of intracellular water. One major adaptation that has allowed the zooplankton persistence across diverse salinities is osmoregulation, a mechanism carried out by mitochondria-rich cells. In branchiopods, these ion-transporting cells make up two structures (1) a basal protrusion known as the epipodite and (2) the nuchal gland, a sensory organ adapted to mediate osmotic homeostasis in freshwater zooplankton (Aladin & Potts, 1995). These components mediate salt exchange between the haemolymph and the water, a function similarly performed by fish gills (Potts & Durning, 1980; Aladin & Potts, 1995). It is important to note that osmoregulatory capacities are specific to each species. For example, *D. magna* and *D. pulex* are both hyperosmotic regulators at freshwater to 8 g L^{-1}, but *D. pulex* becomes isosmotic at higher salinities (Aladin & Potts, 1995). As a result, *D. pulex* can survive in salinities of up to 20 g L^{-1} while *D. magna* is limited to a strict threshold of 8 g L^{-1}. Although the mechanisms controlling osmotic balance in zooplankton are not fully understood, laboratory studies and lake surveys suggest that the osmoregulatory abilities of most species is fairly limited (Aladin & Potts 1995; Martínez-Jerónimo & Martínez-Jerónimo 2007; Liu & Steiner 2017). In addition to problems with osmotic balance, rising salinity levels may also be associated with the formation of harmful precipitates, metal toxicity, and high pH levels, which could all have negative effects on the physiology of zooplankton (Anderson, 1950).

1.4.2. Interspecific variation

In the context of salinization, cladocerans are expected to be especially sensitive compared to other zooplankton. Although some cladocerans can be found in brackish waters, most are solely adapted to lower salinity environments (Arnér & Koivisto, 1993). One study found that the majority of cladocerans surveyed in the northern plains were exclusively present in low salinity lakes (<3 g L^{-1}). This suggests that many cladocerans are stenohaline, capable of withstanding only a narrow salinity range (Hammer, 1993). Many copepods can tolerate a wider range of salinities, and naturally dominate hypersaline lakes due to the absence of their more salinity-sensitive competitors (Wissel et al., 2011; Cooper & Wissel, 2012). These findings suggest that lake salinization in the Great Plains could cause shifts towards halotolerant copepods over cladocerans.

1.4.3. Intraspecific variation

Do all members of a species share the same salinity tolerance? Hutchinson (1967) reported the possibility of intraspecific variation, while speculating on the varied responses to salinity in morphologically similar crustacean populations. Intraspecific differences in salinity tolerance could emerge from the starting point of phenotypic plasticity with subsequent selection pressures resulting in the divergence of populations of the same species through adaptation to local environments (De Jong, 2014). These subpopulations are referred to as ecotypes or clones, describing variants that differ in phenotypes but are still capable of interbreeding (De Jong, 2014; Liu & Steiner, 2017; Carvalho, 1987; Weider & Hebert, 1987).

There has been ample evidence suggesting intraspecific influences on salinity responses in some cladocerans. Weider and Herbert (1987) concluded that *D. pulex* clones from a set of Arctic ponds significantly differed in salinity tolerances by comparing toxicity responses. Similarly, Sinclair and Arnott (2018) found differing salinity responses in two ecotypes of *D. pulex*, possibly due to differences in past salt exposures. Other studies indicated that variants of *D. magna* have salt sensitivities comparable to their natural habitats (Arnér & Koivisto, 1993; Teschner, 1995). For example, brackish clones of *D. magna* can persist in high salinity treatments with greater fitness in saline experimental conditions than freshwater conditions (Teschner, 1995). Additionally, evidence of rapid evolution in zooplankton to salinities suggests high potential for intraspecific adaptations to local environments (Coldsnow et al., 2017). From the perspective of rising salinities, significant differences in salinity tolerances within species could change our understanding of how zooplankton will persist in the Great Plains based on metacommunity theory.

1.4.4. Community effects

The overall consequences of increased salinities for zooplankton communities can be detected by observing biogeographical patterns or through experimental studies. Biogeographical surveys on aquatic invertebrates have shown substantial reductions in taxonomic richness, Shannon diversity and abundance as salinities exceed 1 g L^{-1} (Nielsen et al., 2003; Schallenberg et al., 2003; Wissel et al., 2011). Field experiments yield more ambiguous results possibly due to differences in objectives, methodology or starting species compositions. For example, some studies report that salinities at 1 g L^{-1} significantly decreased species richness (Meter & Swan, 2014; Hintz et al., 2017) whereas one study found that species richness was unaltered by salinities at >2 mg/L (Symons & Arnott, 2013). Some major differences between these studies that make it difficult to compare directly include the salt(s) used (e.g. pure NaCl vs. mixture of chlorides and sulfates) and whether phytoplankton or fish were being investigated in the same enclosures as zooplankton. Sinclair & Arnott (2018) even found conflicting zooplankton responses to salinity increases by 250 mg/L between two lakes, where one community became dominated by littoral species while the other was unaffected, concluding that local context plays a major role in determining salinity tolerance. Overall, these findings suggest that while general trends are clear, responses to salinity may be specific to the zooplankton community under study.

1.4.5. Synergistic effects

The composition of salts in the water, as opposed to total salinity, may also be an important factor for biota. Depending on the watershed geology and sources of water, the ionic compositions of lake water may vary across a region (Covich et al., 1997). For example, $MgSO_4$ and NaCl dominated brines are common to lakes of Saskatchewan (H. Haig, University of Regina, personal communication; Last, 1992). The importance of dominant salt types in brines in influencing biological responses is unclear. In some studies, chloride is considered the primary factor influencing salinity tolerances in cladocerans (Aladin & Potts, 1995; Kefford et al., 2004). However, extreme concentrations of other salts can have varying effects. For example, high calcium and magnesium have been associated with increased salinity tolerance in *D. magna* as water hardness likely improves the imperviousness of cell membranes (Maltby, 2007). If specific salts result in varied stress responses, then past experimental studies that used commercial sea salts to manipulate salinities may have overgeneralized the effects of total salinity (Nielsen et al., 2003; Zalizniak et al., 2006). Other studies suggest the identity of the dominant brine is unimportant. For example, no significant differences were found when Zalizniak et al. (2006) performed acute toxicity studies comparing the stress responses of invertebrates under four different brine types including synthetic ocean mix, sulfate and calcium carbonates, and calcium non-carbonates. In accordance with these results, both Moore (1952) and Wissel et al. (2011) reported that total salinity (all dissolved salts) is the primary factor invertebrate communities in Saskatchewan. These conclusions suggest that investigating the toxicity of salinity could be more important than considering the toxicity of specific ions. The influence specific salts have on zooplankton survivability is evidently complex, but research on the effects of salinity can still be conducted if the artificial salinization method chosen is suitable for the research question.

Other factors that may interact with salinity to influence zooplankton communities include alkalinity and water temperature. Rising salinities in surface waters across North America have been linked with increasing alkalinities, a phenomenon collectively termed "freshwater salinization syndrome" (Kaushal et al., 2018). The joint increase in salinity described at the continental scale by Kaushal et al. (2018) has also been described for the Great Plains (Wissel et al., 2011). Elevated alkalinity in aquatic systems has shown to reduce survivorship in some zooplankton species and increase eutrophication by supplying an excess of inorganic carbon for phytoplankton (O'Brien & deNoyelles, 1972; Boyd et al., 2016). Water temperature may also become a key variable that interacts with salinity to influence zooplankton. Previous studies have found that salinity decreases metabolic rates and reproduction in *Daphnia,* while temperature independently increases the values of these parameters (Heugens et al., 2006; Chen & Stillman, 2012). When combined, increased temperatures reduces salinity tolerance, affecting growth and mortality rates in *Daphnia carinata* (Hall & Burns, 2002). However, contrasting results were reported by Chen & Stillman (2012) who concluded that temperature stress led to increased tolerances to salinity for *Daphnia pulex*. The latter is a more common finding across a range of aquatic organisms called "cross-tolerance" and can be understood as the priming of a protective response to handle a subsequent stressor (Gunderson et al., 2015). Together, these findings suggest that the timing of increased temperatures and salinities could have an influence on how organisms persist in the Great Plains.

1.5. Zooplankton dispersal

Biological dispersal is the movement of individuals or living propagules to a new habitat or population (Allen, 2007). Dispersal can occur during juvenile or adult stages either actively or passively. Active dispersal is movement within the physical capacity of an individual. For instance, birds and insects are effective dispersers due to their flight. Passive dispersal is movement influenced by external force, applicable to sessile plants or animals with limited mobility (Croteau, 2010). After dispersing, the propagule must successfully colonize, as measured by reproduction and persistence in the new habitat. Dispersal can have implications not only for individual fitness, but over time can lead to changes in the gene pool and species distributions.

Aquatic invertebrates have developed a variety of interesting physical structures and behavioural strategies to allow for overland transport to neighboring water bodies (Bassett, 1963). Many cladocerans produce diapausing eggs resistant to desiccation, extreme temperatures and ingestion by predators, which can allow for dispersal across the inhospitable terrestrial landscape. In *Daphnia,* these resting eggs can develop hook-like structures to increase the likelihood of latching onto animal vectors (Havel & Shurin, 2004). Other strategies aimed at improving dispersal rates include the production of floating eggs and the deposition of eggs in shallow waters where water birds and mammals are more likely to pick them up (Allen, 2007).

Some of the most common vectors that move zooplankton among lakes include wind, rain and stream connections (Bilton et al., 2001; Cáceres & Soluk, 2002; Cohen & Shurin, 2003). Winds have been shown to move adult zooplankton or diapausing eggs over short distances (Cáceres & Soluk, 2002; Cohen & Shurin, 2003). Rain as a vector describes storms or flooding events that could connect lakes with adjacent water bodies, thereby providing a vector for movement (e.g. river networks; (Havel & Shurin, 2004). Transport by animal vectors (phoresy) occurs when adult zooplankton attach externally or when eggs survive in the guts and feces of birds, insects, amphibians and mammals (Bilton *et al.*, 2001; Cáceres & Soluk, 2002). Human activities also play a role in dispersal, potentially moving individuals long distances when recreational boats unload waters containing exotic zooplankton into a new habitat (Havel & Shurin, 2004).

The role of zooplankton dispersal in structuring local communities is poorly understood. Some studies have asserted high dispersal rates after observing rapid colonization of newly constructed habitats (Audet et al., 2013; Cohen & Shurin, 2003; Vanschoenwinkel et al., 2008). However, similar studies conducted in other regions have demonstrated relatively low dispersal rates (Jenkins & Buikema, 1998; Jenkins & Underwood, 1998; Allen, 2007). In assessing the genetic structure of zooplankton communities across space, many species have been found to be isolated over relatively short distances, an occurrence likely driven by priority effects or dispersal limitation (Cáceres & Soluk, 2002; Jenkins & Underwood, 1998). Limited dispersal is further evidenced by biogeographical studies that show little change in the distributions of some species since the last ice age (Stemberger, 1995).

Why do studies reach contrasting conclusions about the frequency and extent of zooplankton dispersal in the natural environment? Conflicting results could be caused by region-specific factors that influence dispersal, such as the distance from source pond, dispersal vector type, terrain type, species-specific vagility, and the age of water bodies (Jenkins, 1995; Jenkins & Underwood, 1998; Cohen & Shurin, 2003). For example, Cáceres and Soluk (2002) found that wind and rain were primary dispersal vectors while a recent study with similar treatments concluded that large animals were most important (Allen, 2007). Other explanations include differences in experimental setups that could have resulted in differences in attractiveness of the dispersal traps for animals, or differences in terrestrial faunas in regions where the experiments were carried out, leading to differences in the types of animals available to move zooplankton and their resting stages (Allen, 2007).

1.6. Spatial insurance hypothesis

The spatial insurance hypothesis has been tested in a number of studies with varying conclusions (Loreau et al., 2003; France & Duffy, 2006; Gonzalez & Loreau, 2009; Thompson & Shurin, 2012; Symons & Arnott, 2013). Loreau (2003) used a theoretical model to find that intermediate dispersal rates are necessary for spatial insurance to maximize species diversity and stabilize ecosystem functioning; a result later supported by an experimental study (Howeth & Leibold, 2010). In contrast, Thompson and Shurin (2012) concluded that spatial insurance due to metacommunity dynamics can only resists ecological changes caused by specific stressors. They found negligible insurance effects for zooplankton under salinity stress, but this may have been due to the community composition in their region of study or stress experienced during collection which limited the success of immigrants to salt-stressed communities (Thompson & Shurin, 2012).

The ability of dispersal to buffer against salinity-driven changes in zooplankton community structure in Great Plains' lakes relies on two untested assumptions: 1) That variation in salinity tolerance exists in zooplankton distributed across a landscape of lakes with varying salinities; and 2) That dispersal rates are high enough to increase genetic variation in recipient communities or to replace the loss of salinity intolerant individuals. Past studies show that the dispersal of individuals facilitates gene flow among lakes, diversifying gene pools and the genetic composition of the population (Berg et al., 2010). This process catalyzes adaptation to environmental stress, assuming a fraction of the zooplankton immigrants survive to produce offspring in their new habitat (Symons & Arnott, 2013). If salinity-tolerance is a geneticallydetermined trait that varies among populations, the same reasoning should apply for zooplankton populations facing salinity stress.

Recent work by Coldsnow et al. (2017) shows that salinity tolerance in *Daphnia* can evolve over many generations, supporting the idea that there is some degree of genetic control over osmoregulation. In addition, a study by Weider & Hebert (1987) demonstrated differences in salinity tolerance among *D. pulex* clones collected from water bodies of varying salinities. Clones collected from lakes with higher salinities were more resistant to elevated salinity levels in acute toxicity experiments (Weider & Hebert 1987). The same resistance can be found in *D. magna* of the Baltic Sea, adapted to surviving saline waters of 12.5 g L^{-1} compared to a freshwater clone that can tolerate salinities only below 4 g L^{-1} (Arncr & Koivisto, 1993; Schuytema et al., 1997). This broad range in salinity tolerance can be explained by the presence of interspecific differences among clones caused by environmental and genetic variance. In addition to the replacement by similar species, intraspecific differences provide another means of replacement in communities that undergo functional losses caused by salinity stress. For example, zooplankton communities can be further stabilized if a salinity-tolerant *Daphnia* disperses and replaces the loss of a more sensitive clone. The significance of clonal variation in salinity tolerances has yet to be studied for the Great Plains but could have implications for spatial insurance.

The second assumption stated above, regarding the rate of dispersal of zooplankton across the landscape, is more difficult to evaluate. As discussed previously, there is disagreement in the literature on the effective rates of zooplankton dispersal in natural habitats. The highest rates of dispersal among lakes have been found in interconnected bodies of water (Michels et al., 2001). Given that many lakes on the Great Plains are endorheic and lack stream connections, they will be limited to lower rates of dispersal by means of wind, rain and waterfowl (Jenkins & Underwood 1998). In theory, if dispersal rates are high enough, the simple arrival of individuals, independent of their genetic contribution could forestall local extinction events (Gotelli 1991; Howeth & Leibold, 2010). From a metacommunity standpoint, a lake of increasing salinity might become a sink habitat for salinity-intolerant species. These salinity intolerant species would then solely persist by immigration from surrounding source habitats (i.e. the rescue effect (Brown & Kodric-Brown, 1977).

1.7. Measuring change

Three metrics often used in ecology to describe the structure of communities are species richness, species evenness and species diversity (Stirling & Wilsey, 2001). Although simple, these metrics are assumed to convey important information about communities, as numerous laboratory and field studies have suggested that changes in biodiversity that are reflected by these metrics can have implications for ecosystem structure and functioning (Gotelli & Colwell, 2001, 2011; Hooper *et al.*, 2006). A decrease in species richness can destabilize local ecosystem services whereas reductions in diversity have been linked to ecosystem stability, primary productivity and the strength of species interactions (Cardinale et al., 2012; Heip & Engels, 1974.; Kremen, 2005).

The simplest index of community structure is species richness (S), defined as the number of species present. Despite its intuitive nature and definition, the actual estimation of how many species are present in a local community is a difficult process. Realistically, species richness can only be calculated according to the observed number of species in sample and so the estimate will always be inaccurate due to undersampling (e.g. more species are found with a larger number of samples). A popular method used to correct for this bias when comparing richness values among sites is to use rarefaction to correct for sample size. Rarefaction computes random species assemblages with data drawn from actual community data, constructing a curve that plateaus as sample sizes increase (Gotelli & Colwell, 2011).

The Shannon diversity index (H') is measured based on the relative abundances of species (evenness) and the number of species in a given location. An important application of calculated diversity is to study environmental impacts. Standard measures of diversity are used in field studies to compare communities before and after exposure to a stressor or between different habitats (Heip & Engels, 1974). The index is calculated as shown below, described as the sum of the proportion of species richness comprised of ith species (p_i) multiplied by the natural logarithm of that same value, multiplied by 1 (Shannon, 1948).

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \qquad [1]$$

Evenness describes whether species are found in relatively equal abundances or if the community is dominated by one or a few species, with values ranging from 0 (lack of evenness) to 1 (complete evenness). When coupled with diversity, evenness is a measure often used to compare sets of communities to show abundance disparities. Pielou's evenness (J') is the most common index in ecology of this nature and can be calculated using Shannon diversity (H') and species richness (S) as follows (Alatalo, 2016):

$$E_H = \frac{H}{H_{max}} = \frac{H}{\ln S} \qquad [2]$$

Recently, the usage of these biodiversity measures to study environmental impacts has been criticized because they fail to consider the characteristics of the species found in communities. As a result, studies of zooplankton communities have shifted away from pure taxonomic approaches to understanding community structure towards classifications that depend on the ecological roles played by a species (Barnett et al. 2007). These roles define variation in species' morphology, physiology and phenology as well as describing interactions with other species and with resources (Petchey et al., 2009). This approach allows for more flexible perspectives since niches can be shared between related species and then linked to ecosystem functioning and processes (Pomerleau et al., 2014). For example, zooplankton can be classified by feeding type to evaluate the relative abundance of filter-feeders, stationary suspension feeders, and raptorial feeders. Other traits of interest for zooplankton may include trophic group (i.e. herbivore), predator avoidance behaviour, and average adult body length (Barnett et al. 2007).

The leading framework in calculating functional diversity uses an assemblage of species traits, chosen by the context of the research (e.g. the predicted impacts of salinity on zooplankton ecology), to calculate three functional metrics. The first metric is functional evenness (FEve), described as the spacing between species (Villéger et al., 2008). For example, the clumping of species in trait space will produce a value closer to 0 (uneven) than 1 (even). The second metric, functional richness (FRic), is defined as the convex hull volume between species in the plot (the minimum volume required to contain all points). Communities with low functional evenness or richness are more vulnerable to threats (e.g. invasions, productivity) due to the inefficient usage of resources. The third metric is Rao's quadratic entropy (FD_Q), a functional diversity measure based on the dissimilarity between functional traits and their abundances (Botta-Dukát, 2005; Obertegger & Flaim, 2015; Ricotta et al., 2014). In mathematical terms, this index calculates a single value by the sum of pair-wise functional distances weighed by their relative abundances (Pomerleau et al., 2014) for a community assemblage. The equation involves S as species and d_{ij}

as the dissimilarity between the i-th and the j-ith. For example, the value of d_{ii} is equal to 0 (Botta-Dukát, 2005).

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_i \qquad [3]$$

All functional measures discussed are sensitive to missing trait values (Lefcheck et al., 2015).

Multivariate ordination techniques such as principal component analysis are another approach to describing change in the structure of communities (Abdi & Williams 2010). Ordination techniques simplify (reduce dimensionality) large datasets by converting correlated values to a set of linear uncorrelated values that can be plotted in a two- or three-dimensional ordination diagram (biplot). A two-dimensional biplot of the first two principal components will then display the data in an orientation that conveys information about the differences in community structure among sites (Abdi & Williams 2010). Points located closer together on the plot represent sites that share similar communities, while those further apart have a different community structure. Multivariate analyses such as PCA are sensitive tools for revealing changes in community structure that otherwise could not be identified using univariate statistics.

Understanding how freshwater zooplankton will respond to salinization involves measuring change in a multitude of ways. This project aims to examine changes to community structure and diversity and to test if dispersal can buffer against those changes. The following chapter will describe the experiments I conducted to assess the effects of rising salinities in the Great Plains on zooplankton communities with a focus on dispersal as a moderating force.

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1.9. Figures

Figure 1.1. Map of the North American Great Plains (shaded area) in the United States and Canadian prairies. Bolded states contain watersheds in the American Great Plains that are undergoing significant increases in salinity and alkalinity as reported by Kaushal et al. (2018). The star indicates my main study site (Kenosee Lake) situated in Moose Mountain Provincial Park, Saskatchewan (to be discussed in the Chapter 2).

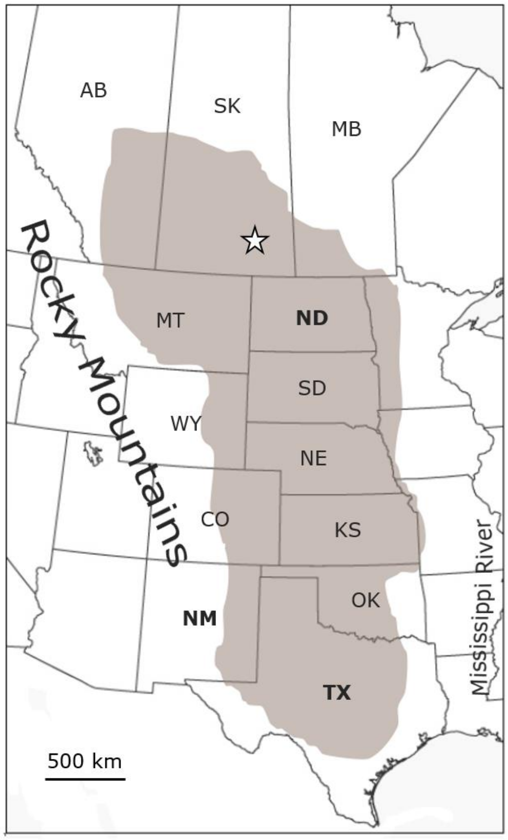


Figure 1.2. Map of Kenosee Lake located in southern Saskatchewan, Canada. The red dot indicates the area of Saskatchewan where Kenosee Lake is found while the blue dot indicates the area where experimental enclosures were set up.

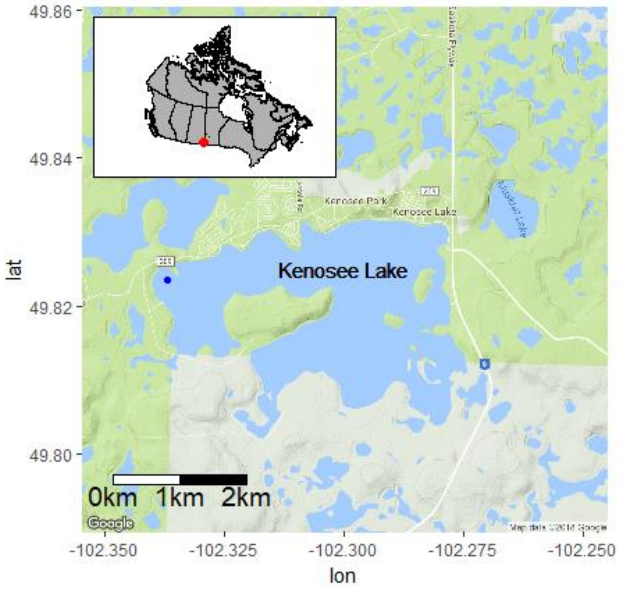
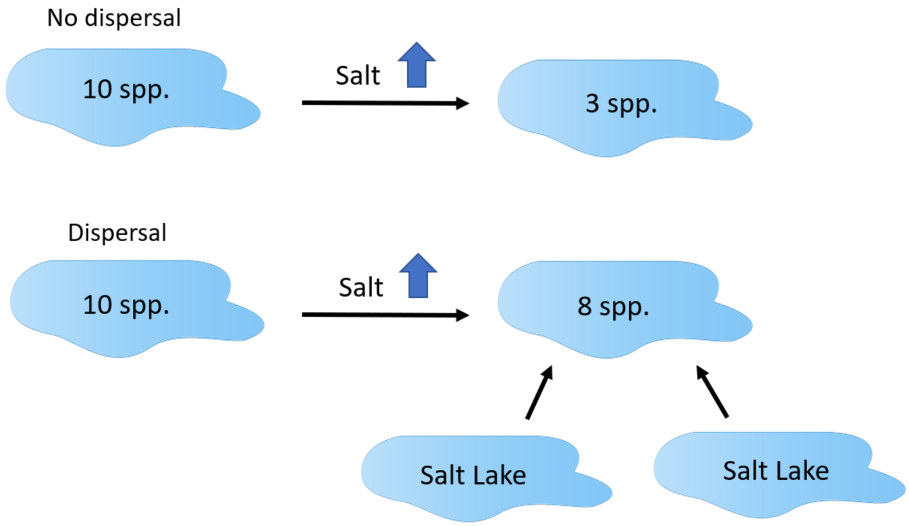


Figure 1.3. Schematic diagram of how spatial insurance could buffer against zooplankton community change in the face of increasing salinities (salinity increases from left to right). Blue shapes indicate lakes and numbers inside indicate species richness. In the absence of dispersal, species are lost without compensation. When dispersal is present, lost individuals or species can be replaced by salinity-tolerant individuals from adjacent lakes.



Chapter 2
Experiments

Can dispersal buffer against salinity-driven zooplankton community change in Great Plains' lakes?

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2.1. Summary

1. The North American Great Plains contains thousands of lakes that vary in salinity from freshwater to hypersaline. Paleolimnological studies show that salinity levels in these lakes are tightly linked with climate, and current projections point to a more arid future in the region due to anthropogenic climate change.
2. Many zooplankton species are sensitive to changes in salinity, and their position near the base of the aquatic food web makes it important to understand how they might respond to increasing salinity levels. Zooplankton communities in lakes with rising salinity levels may exhibit changes in structure, including a shift toward more salinity-tolerant species and a reduction in abundance, species richness, and diversity. However, it is possible that dispersal of zooplankton among lakes, coupled with local adaptation to salinity levels and taxonomic and functional redundancies in the regional species pool, could compensate for losses of sensitive zooplankton in lakes undergoing salinization.
3. To test this hypothesis, a field enclosure experiment was conducted at a freshwater lake in southern Saskatchewan where salinity levels and zooplankton dispersal were artificially manipulated. We found that increasing salinity levels in our enclosures above that in our study lake resulted in lower zooplankton abundances and species richness levels, primarily due to the loss of cladoceran species. However, if enclosures with moderate salinity levels (2.5, 5.0 g L^{-1}) received immigration from nearby lakes, they sustained zooplankton communities with a balanced mix of cladocerans and copepods.
4. Our results provide some evidence that the dispersal of individuals among lakes could reduce salinity-induced changes in zooplankton communities. The maintenance of cladocerans in treatments that received immigrants may have been driven by either a

rescue effect or the introduction of salinity-tolerant cladocerans from surrounding lakes. We ran laboratory toxicity assays using *Daphnia* collected from lakes within the region and found that intraspecific variation in salinity tolerance does exist, providing evidence that the latter explanation may be plausible.

5. Given the importance of dispersal for zooplankton communities responding to elevated salinity levels, it will be important to preserve regional biodiversity and the mechanisms and pathways that allow for dispersal of individuals among lakes and ponds on the Great Plains.

2.2. Introduction

The salinity of surface waters is increasing throughout North America (Dugan et al. 2017). These increases have been caused by a combination of road salt and agricultural runoff, changes in the amount of impervious land cover, and climate-driven changes in precipitation and evaporation rates (Covich et al., 1997; Dugan et al., 2017; Kaushal et al., 2018; Schallenberg et al., 2003; Williams, 1999). While the increases in salinity over the last two decades have been modest, some studies have reported that even small increases in salinity can have significant impacts on the biodiversity of freshwater lakes (Cooper & Wissel, 2012; Schallenberg et al., 2003; Van Meter et al., 2011; Williams, 1999; Wissel et al., 2011). At sublethal thresholds, freshwater organisms face higher osmoregulatory costs which can alter life history parameters such as lifespan and reproductive rates (Martínez-Jerónimo & Martínez-Jerónimo, 2007). High salinities can lead to losses of key species and changes in community dynamics and ecosystem function (Corsi et al., 2010; Hintz et al., 2017; Kefford et al., 2016; Nielsen et al., 2003).

While increases in salinity due to road salt application are a near-term concern and have been the focus of intense media interest, climate change is also expected to have a significant impact on lake salinity levels in the coming decades (Williams, 1999; Wissel et al., 2011; Dugan et al., 2017). Climate-driven changes in salinity are especially concerning for lakes in the Great Plains of North America, where decreased precipitation and rising temperatures are expected to increase the frequency of droughts (Dai, 2013; O'Reilly et al., 2015; Sauchyn et al., 2002). The landscape in this region is dense with surface waters that have salt concentrations ranging from freshwater (<1 g L^{-1}) to many times above oceanic salinities (up to 400 g L^{-1}; Last & Ginn, 2005; Wissel et al., 2011). Many of these lakes are endorheic (closed basin) lakes which receive water primarily from precipitation, making them very sensitive to changes in precipitation levels (Van Der Kamp, Keir & Evans, 2008; Wissel et al., 2011). Paleolimnological studies in the region show that lake salinity levels regularly fluctuate, rising during drought conditions and falling during periods of above average precipitation (Fritz et al., 2000; Michels et al., 2007). In response to models that predict drier conditions for the prairies in the coming decades (Sauchyn et al., 2002; Dai, 2012), there has been increased interest in understanding how salinization will impact water quality and biota for the region's lakes (Covich et al., 1997; Williams, 1999; Fritz et al., 2000; Wissel et al., 2011; Cooper & Wissel, 2012).

One group of organisms that may be impacted by rising salinity levels in Great Plains' lakes are zooplankton. Zooplankton are aquatic microinvertebrates that occupy the lower levels of the aquatic food web. They feed on periphyton and phytoplankton and are important prey items for larger invertebrates and young fish (Thompson, 2012). A synoptic survey of 70 lakes in the Great Plains concluded that salinity is the primary force structuring zooplankton communities in this region (Wissel et al., 2011). Low salinity lakes have a mixture of cladocerans, calanoid copepods, and cyclopoid copepods, while high salinity lakes (> 3.5 g TDS L^{-1}) contain only harpacticoids and *Artemia* (Wissel et al., 2011). Past studies on aquatic ecosystems in other parts of the world have also found that higher salinity levels are associated with lower taxonomic richness, diversity, abundance, and biomass of zooplankton, and that salinization can cause shifts in community composition toward halotolerant species (Schallenberg et al., 2003; Wissel et al., 2011; Thompson & Shurin, 2012; Hintz et al., 2017). The results of many laboratory-based studies confirm that most freshwater zooplankton have a low tolerance to dissolved salts (EPA, 1988; Arnér & Koivisto, 1993; Martínez-Jerónimo & Martínez-Jerónimo, 2007). Therefore, both distributional data and laboratory assays suggest that freshwater zooplankton communities are sensitive to salinity levels, indicating that communities may change as salinities increase in Great Plains' lakes.

Theory and manipulative experiments have indicated that when zooplankton communities are faced with a changing environment, dispersal of individuals within the regional metacommunity can act to buffer against structural and functional changes at the local level (Klug *et al.*, 2000; Cottenie & De Meester, 2004; Binks, Arnott & Sprules, 2005; Keitt & Fischer, 2006; Thompson & Shurin, 2012; Symons & Arnott, 2013). Within a regional species pool, multiple species may have overlapping taxonomic representation and functional roles such that individuals from the larger metacommunity could substitute for a loss in a local community (Loreau et al., 2003; Cottenie & De Meester, 2004; Symons & Arnott, 2013). In the case of salinity change, dispersal could minimize taxonomic and ecological changes by allowing salinity-intolerant organisms to be replaced by salinity-tolerant groups that are functionally or taxonomically similar. For example, one species of *Daphnia* could be replaced by another, or a salinity-tolerant genotype of a *Daphnia* species could replace a salinity intolerant member of the same species. Under this scenario, overall ecosystem function and zooplankton community structure might be unaffected by salinization despite changes to the list of species or genotypes present. The likelihood that dispersal could act to counter salinity-driven changes in this manner depends on two assumptions: (1) That dispersal occurs at a temporal and spatial scale that is significant enough to compensate for losses; and (2) That variation in salinity tolerance among individuals and species occurs among lakes with varying salinity levels. It is difficult to evaluate assumption one without field studies in the region of interest, as published studies on zooplankton dispersal differ widely in their conclusions about dispersal rates (Audet et al., 2013; Cohen & Shurin, 2003; Havel & Shurin, 2004; Jenkins & Underwood, 1998; Jenkins, 1995; Márquez & Kolasa, 2013; Vanschoenwinkel et al., 2008b). Some past studies support assumption two, as there is evidence that zooplankton can evolve to tolerate higher salinity levels (Coldsnow et al., 2017) and that there are differences in salinity tolerance both within and among species (Weider & Hebert, 1987; EPA, 1988). Manipulative experiments also provide some support for dispersal acting as a buffer against community change in the case of rising salinities (Thompson & Shurin, 2012; Symons & Arnott, 2013) and for zooplankton communities exposed to several other stressors such as nutrient enrichment (Forrest & Arnott, 2006), acidification (Steiner et al., 2011) and introduced predators (Howeth & Leibold, 2010).

Although there have been some excellent studies examining the response of zooplankton communities to rising salinities, we are not aware of any that have been conducted in a region like the Great Plains where salinity is highly variable over space and time. As a result, the magnitude of the salinity changes tested in previous studies were quite small (<1 g L^{-1}), paling in comparison to the spatial and temporal heterogeneity in salinity levels experienced for prairie lakes. In addition, the animals used in these other studies were unlikely to have an evolutionary trajectory influenced by the fluctuating salinity levels characteristic of lakes in this region. In this study, we conduct a field enclosure experiment to test if dispersal among prairie lakes could act to buffer zooplankton communities against salinity-driven changes. We manipulate dispersal and salinity levels in our enclosures and examine how community structure and functional composition of zooplankton changed over a six-week experiment. In addition, we perform laboratory toxicity experiments to test if intra- and interspecific variability in salinity tolerance is detectable for common zooplankton species collected from prairie lakes. Our results show that there is variability within and between species in terms of salinity tolerance, and that dispersal can buffer against changes in community structure if salinity increases are moderate (2.5-5.0 g L^{-1}). However, communities exposed to higher salinity levels (7.5 g L^{-1}) changed even though they received a regular influx of dispersers from nearby brackish lakes.

2.3. Materials and methods

2.3.1. Field study

Treatments

Our field experiment was conducted over a six-week period on Kenosee Lake (49.827°N, 102.299W) in Moose Mountain Provincial Park, Saskatchewan, from June to early August 2017. Figure 2.1a provides a timeline for the experiment. A series of floating polyethylene enclosures were deployed on the lake and each enclosure was filled with ~1178 L of unfiltered lake water to stock zooplankton communities at natural densities. The experiment consisted of eight unique treatments, replicated three times for 24 enclosures in total (Figure 2.1b). The four salinity treatments were 0.95 (ambient control), 2.5, 5.0, and 7.5 g L^{-1}. This range was chosen based on LC_{50} values of common zooplankton taxa expected to be found in the Great Plains, and is easily within the range of climate-driven salinity level change documented from paleolimnological studies of lakes in the region (Kefford et al., 2004; Laird et al., 1998; Martínez-Jerónimo & Martínez-Jerónimo, 2007; Michels et al., 2007; Mount et al., 1997). The salt formulation added to enclosures was based on the average chemical composition of saline lakes in the Northern Great Plains (Table 1; Last, 1992). To achieve the final desired salinity in each enclosure, salt was added gradually in increments of 2.5 g L^{-1} per day (Figure 2.1b).

The four salinity treatments were crossed with two dispersal treatments: passive and active, where the latter would be regularly stocked with fixed volumes of zooplankton collected from lakes with salinity levels higher than Kenosee Lake (hereafter referred to as 'dispersers'). Our rationale was that these lakes would contain zooplankton adapted to living under elevated salinity levels. To obtain dispersers for our dispersal treatments, zooplankton were collected and added every 10 days using a 30 cm, 63 µm conical zooplankton net from three donor lakes: Big Quill Lake (51.871N, 104.383W), Peter Lake (51.461N, 104.926W) and an unnamed lake at 49.697N, 102.204W. The salinities of these lakes were 5.6, 3.5, and 1.5 g L^{-1}, respectively. The zooplankton samples were kept in 10 L carbuoys filled with filtered lake water and placed in coolers with ice packs for transport to enclosures on Kenosee Lake. Dispersers from the three lakes were combined, gently homogenized, and then introduced to the dispersal treatments at a concentration that represented a dispersal rate of approximately 1% of ambient zooplankton abundance per day (i.e. 1% of population size in each enclosure). This dispersal rate was chosen with reference to a previous study that found a 0.01 - 0.63% daily total zooplankton dispersal rate between interconnected ponds (Michels et al., 2001). The dispersal level we used is likely significantly higher than for natural rates among unconnected water bodies but was selected to maximize the potential of observing an effect over our relatively short six-week experiment. The passive dispersal treatments did not receive any dispersers collected from donor lakes but did receive filtered water from these lakes in volumes that matched the inoculum for the dispersal treatments (~ 5 L). Dispersers were added to enclosures on day 11, 21 and 31 (Figure 2.1a). On each of these occasions, three replicate aliquots of dispersers were collected and preserved in 95% ethanol to examine the taxonomic composition of animals being introduced to the dispersal treatments.

Sampling and identification

To examine the changes in zooplankton community structure through time, zooplankton samples were collected from enclosures after the experiment was fully set up (day 10) and at the end of the experiment on day 42. Samples were collected from the middle of each enclosure by conducting a vertical tow with a 15 cm diameter, 80 µm conical zooplankton net. Based on the net diameter and the length of the tow, we collected approximately 3% of the zooplankton population from each enclosure at each sampling date. Samples were preserved in 95% ethanol and transported to the laboratory for enumeration. Salinity and pH levels were measured in each enclosure at the time of zooplankton sampling using a handheld Cole-Parmer PC100 pH Conductivity Meter. The salinity levels remained relatively consistent during the first four weeks of the experiments (expected salinity for each treatment ± 0.81 g L^{-1}) but dropped approximately 1.0 g L^{-1} in the final two weeks of the experiment due to heavy rains.

Taxonomic guides and primary literature sources were consulted in identifying most zooplankton to the species level. *Skistodiaptomus oregonesis* and *Skistodiaptomus reighardi* were grouped together, as were the close relatives *Daphnia pulicaria, D. schodleri* and *D. pulex,* which were identified as *D. pulicaria* due to modern taxonomic changes. The main resources used were the Image-based Key to North American Zooplankton by Haney *et al.*, (2013), and two identification guides by Balcer et al. (1984) and Witty (2004). Zooplankton samples were placed on a Ward counting wheel for enumeration using a dissecting microscope. When required, individual animals were transferred to a glass microscope slide and examined at higher magnification under a compound microscope. Immature copepods were classified as either copepodites or nauplii and were not identified further.

Choosing functional traits

Functional diversity of communities is often associated with ecosystem functioning, making it an important consideration in the context of community change (Villéger et al. 2008). To examine changes in the functional metrics of the zooplankton communities in our enclosures, we gathered information on habitat preference, trophic group, feeding type, and mean body length. A complete trait table was derived from a review study by Barnett et al. (2007) that used online databases to investigate freshwater zooplankton species in North America. Other sources were consulted for trait data on *Microcyclops rubellus* (Enríquez García et al., 2009; Gutiérrez-Aguirre et al., 2016; Thompson et al., 2015). Trophic group describes three feeding preferences on an ordinal scale: herbivore, omnivore, and omnivore-carnivore. Classes with two categories represent intermediate stages (Vogt et al., 2013). Habitat preference indicates whether species generally occupy the pelagic or littoral zone. Feeding strategy is grouped into six types: B-filtration, D-filtration, C-filtration, S-filtration, raptorial, or stationary suspension. Assignment to feeding style categories depended on which body features support the filtering mechanism and whether the species is an active or passive feeder. Mean body length was also included as it can be associated with feeding interactions and productivity (Barnett et al., 2007).

Statistical analyses

To visualize differences in community structure among our enclosures, a principal component analysis (PCA) was performed on Hellinger transformed species abundances using the prcomp function in the stats package for R (R Core Team 2018). Following recommendations by Lepš and Šmilauer (2003), rare species were removed before the analysis if they were not present in at least 20% of samples (<9 enclosures).

To compare species richness and species diversity among enclosures, we used indices that account for differences in the number of individuals identified among enclosures. For richness, we used rarefaction to calculate values that reflect sampling effort for each enclosure (Hurlbert, 2006). Rarefaction accounts for differences in sampling effort by resampling abundance data for a particular site thousands of times to determine the average number of species identified for a given number of individuals collected (Gotelli & Colwell, 2001). We rarefied communities to 98 individuals, which was the lowest number of individuals identified from a single enclosure. Rarefaction was conducted using the rarefy function in the "vegan" package for R (Oksanen et al. 2017). Similarly, the diversity index used corrected for differences in taxonomic/sampling effort. Diversity was calculated according to Chao's method for calculating rarified Hill numbers (Chao *et al.*, 2014). We used the estimateD function in the iNEXT package for R to calculate rarified order 1 Hill numbers representative of the exponential of Shannon's entropy index (Hsieh et al., 2016).

To calculate functional measures of richness, diversity, and evenness, we used the dbFD function in the FD package in R (Laliberté et al. 2014). The functional richness and evenness calculations in this package are based on Villéger et al. (2008). We used Rao's quadratic entropy as the measure of functional diversity (Botta-Dukát, 2005). To correct for sample size differences among enclosures that might bias estimates of functional richness or diversity, we used a bootstrap approach for their estimation. The bootstrap was run 1000 times and each time a random selection of 98 individuals was selected from each enclosure to calculate functional richness and diversity. We then took the average of the 1000 bootstraps to arrive at the functional richness and diversity values for each enclosure.

The effects of salinity and dispersal on various community metrics were tested using 2-way ANOVAs. The metrics included three taxonomic diversity indices (rarified species richness, Hill diversity, evenness), and their functional counterparts (functional richness, Rao's quadratic diversity and functional evenness), as well as total abundance. Immature copepods and nauplii were removed in the calculation of all diversity indices since they were not identified to the species level. Assumptions of normality were tested by plotting a histogram of the residuals and a Levene's test was conducted to ensure data met the assumption of equal variances (all assumptions were met). A post hoc analysis using Tukey's Honest Significant Difference test was performed when ANOVA results were significant. For the ANOVAs, we expected to find differences among treatments based on salinity and dispersal but were most interested in the interaction between these two factors. A significant interaction could indicate that the effect of salinity on our response variables depended on dispersal, such that active dispersal treatments maintained higher levels of richness or diversity while those not receiving dispersers experienced decreases.

A power analysis was conducted to determine the statistical power we had to detect differences among our treatments based on the variability of our response variables within and among treatments. The power analysis was run for both rarified richness and Hill Diversity. The analysis was carried out by way of bootstrap simulations in R. Briefly, during each bootstrap (repeat) a simulated dataset with known differences among treatments was created. The simulated data for each treatment was created by drawing a random number from a normal distribution given mean and a standard deviation values that matched the data found in our experiment. So, for example, in one run of the simulation, the mean species richness could be 10 in the active dispersal treatment and 9 in the passive dispersal treatment. The rnorm function in R would then be used to create the simulated dataset with means of 9 or 10, depending on treatment, with variability matching that found in the real experiment. The simulation is then run 1000 times and the proportion of times the p-value is significant is the statistical power (since we know a real difference existed because the data were simulated). For each factor (dispersal, salinity) and their interaction, a plot was generated to show the statistical power to detect a difference in richness or diversity between 0 and 100%.

2.3.2. Laboratory experiments

In July 2018, two sets of clones of *D. pulicaria* and *C. sphaericus* were collected from several lakes in North Dakota with varying salinity levels (Table 5). Samples were brought back to the laboratory to establish monospecific cultures for use in acute toxicity tests. Animals were cultured in COMBO medium (Kilham et al. 1998) with added NaCl to match resident lake levels and avoid osmotic shock. Cultures were housed in an environmental chamber with a 12-h light and 12-h dark cycle under a temperature range of 24°C to 26°C. Cultures were fed weekly with live *Chlamydomonas reinhardtii* algae that was cultured in a 0.01:1 mixture of Bold's Basal Medium and COMBO. Before toxicity tests were conducted, cultures were reared through at least five generations to minimize maternal or environmental effects (Coldsnow *et al.*, 2017). Individuals with a similar size were selected for assays to minimize age-specific tolerances. For each assay, 10 individuals were placed in a 120 mL beaker. The medium in the beaker was COMBO adjusted to increasing salinities by the addition of NaCl according to species-specific treatment conditions (*Daphnia* were generally more salinity-tolerant than chydorids, so received salinity treatments with a higher range). The animals were observed after 48 hours and a 48-h effective concentration (EC50) was calculated for each species using the "drc" package in R (Ritz et al., 2015). The EC50 for this study was defined as the concentration needed to immobilize 50% of the individuals after two days. The assays were replicated three times for each species collected from each lake.

2.4. Results

Community changes

At the beginning of the experiment, communities were not structured by either of our treatment variables. At the conclusion of the experiment, communities in the passive dispersal enclosures were structured along PCA axis 1 by salinity. Low salinity treatments (1, 2.5 g L^{-1}) contained a mixture of cladocerans and cyclopoid copepods, while high salinity treatments (5, 7.5 g L^{-1}) shifted toward communities dominated by the calanoid copepods *Skistodiaptomus pallidus* and *Leptodiaptomus sicilis* (Figure 2.2a). This interpretation is supported by the abundance data which show cladocerans outnumbering copepods in low salinity passive dispersal treatments, but not at the highest salinity (7.5 g L^{-1}, Figure 2.3). In contrast with those results, active dispersal treatments did not show a clear gradient in community structure related to salinity at the conclusion of the experiment, with the exception of the highest salinity treatment (7.5 g L^{-1}), which grouped apart from the other enclosures in the ordination (Figure 2.2b). In addition, cladocerans remained numerically dominant in active dispersal enclosures

(Figure 2.3). Some of the cladoceran species which remained abundant in elevated salinity active dispersal enclosures (*D. rosea, D. pulicaria* and *D. mendotae*) were present in lakes from which dispersers were collected.

Richness, abundance, diversity, and evenness did not differ significantly among our enclosures at the beginning of the experiment (Two-way ANOVAs; p-values>0.05). Samples from the end of the experiment showed that salinity had a significant affect on richness, but not abundance, diversity, or evenness of the communities (Table 3). The dispersal treatment (active or passive) did not significantly affect any of the univariate metrics except for functional evenness (Table 3). Despite the lack of a significant interaction between salinity and dispersal in the ANOVAs, the patterns for abundance and evenness were compelling, with both variables appearing to decline with increased salinity in the passive but not active enclosures (Figure 2.4).

Salinity and dispersal interacted to determine functional evenness, with communities in active dispersal enclosures maintaining evenness at elevated salinity levels, while communities in passive dispersal enclosures became more uneven (Figure 2.5; Table 3). Functional richness and Rao’s diversity showed no significant differences among treatments (Figure 2.5; Table 3).

Power analysis

Based on the number of replicates in our experiment and the variability of communities among our enclosures, our experiment had a high power (≥0.8) to detect a statistically significant difference for species richness if there was a difference in richness among treatments of 30%, 25%, and 65% for salinity, dispersal, and their interaction, respectively (Figure 2.6). For species diversity, a high power would have been achieved with differences in diversity values of 50%, 40%, and >90% for salinity, dispersal, and their interaction (Figure 2.6).

EC50 values

A one-way ANOVA indicated significant differences in EC50 values for *D. pulicaria* collected from lakes with differing salinities, with those collected from the higher salinity lake having a higher tolerance for salinity (P<0.01; Figure 2.7a). EC50 values did not differ for clones of *C. sphaericus* collected from lakes of differing salinities (P = 0.67; Figure 2.7b).

2.5. Discussion

Our experiments provided evidence that dispersal of individuals among lakes could reduce salinity-induced changes in zooplankton communities, suggesting that overall community structure could be maintained in the case of moderate salinity increases. Communities exposed to elevated salinities that did not receive augmented dispersal from surrounding lakes experienced a decrease in cladoceran abundances, resulting in communities dominated by copepod species. In contrast, communities that received augmented dispersal contained a balanced mix of cladocerans and copepods despite exposure to increased salinity levels. Studies conducted with zooplankton from other regions and at much lower salinity levels have also reported a significant role for dispersal in maintaining cladocerans in salt-stressed communities (Thompson & Shurin, 2012; Sinclair & Arnott, 2018). The maintenance of cladocerans in enclosures that received dispersal could be the result of two distinct processes: 1) a rescue effect; or 2) the introduction of salt-tolerant clones or species to the community. If the maintenance of cladocerans can be solely attributed to the rescue effect, then the response we found could simply be the result of immigration boosting population sizes and lowering the probability of extinction due to demographic and environmental stochasticity (Brown & Kodric-brown, 1977). Under that scenario, waterbodies with increased salinity levels would remain suboptimal sink habitats where mortality exceeds reproduction. Alternatively, cladocerans such as *Daphnia* may have persisted in elevated salinity treatments due to the arrival of salt-tolerant clones sourced from our dispersal lakes. Our laboratory studies of NaCl toxicity showed that salinity tolerance can differ between clones of *D. pulicaria* found on the Great Plains, demonstrating the plausibility of this mechanism. In addition, several studies conducted in other regions have reported significant differences in salt sensitivity among clones of other *Daphnia* species, including *D. pulex* and *D. magna*, likely due to their history of exposure to elevated salinity levels (Weider & Hebert, 1987; Arnér & Koivisto, 1993; Teschner, 1995; Sinclair & Arnott, 2018).

Univariate measures of community structure did not show consistent patterns of change in response to salinity and dispersal. We expected the ANOVAs for abundance, richness, diversity, and evenness to reveal significant interactions between salinity and dispersal, such that communities that received dispersal would maintain values for these metrics that mirrored control treatments, while those without dispersal would see significant changes. Instead, the only significant result we obtained was for salinity driving reduced species richness; a result that was expected based on previous surveys conducted in the region (Wissel et al., 2011). Our failure to detect an interaction between salinity and dispersal suggests either that dispersal was unable to buffer against change in these metrics, or that we simply did not have the statistical power to detect such a phenomenon. We lean toward the latter explanation, as we believe there are some patterns in our results for richness and diversity that suggest these metrics were stable for dispersal-augmented communities exposed to moderate salinities (2.5, 5.0 ‰), but declined in communities exposed to those same salinities without dispersal (Figure 2.3). Our power analyses showed that the interaction between salinity and dispersal would have needed to lead to a difference of at least 65% for richness and >90% for diversity in order for our ANOVAs to achieve a high statistical power (80% probability of rejecting a false null hypothesis; (Cohen, 1988). In our actual experiments, the largest difference in richness and diversity that could have driven an interaction were on the order of 25-30% (Figure S1), which means we had relatively low power to detect this type of relationship (Figure 2.6).

Of our functional metrics, only functional evenness showed a relationship with the two factors in our experiment. Dispersal appeared to successfully counter salinity-driven reductions in functional evenness by maintaining cladocerans in elevated salinity treatments, thereby allowing for a more even distribution of both cladocerans and copepods (which tend to have different trophic groups and feeding types) in functional space (Villéger *et al.*, 2008). The lack of a response of functional richness and diversity to elevated salinity levels was surprising given that taxonomic richness declined with salinity in our experiment. The results for richness and diversity could mean that elevated salinity levels have little effect on the distribution of functional traits in zooplankton communities, but we were only able to obtain complete information for four functional traits, providing a very coarse outline of the potential variation in functional traits among the communities in our enclosures. Studies of changes in functional diversity for zooplankton communities would benefit greatly from some basic ecological research to define and categorize functional traits for common freshwater zooplankton.

When simulating dispersal during our enclosure experiments, we chose a dispersal rate of ~1% of the resident community abundance per day – a level chosen based on studies of an interconnected pond system (Michels et al., 2001) and our desire to test our hypotheses within a reasonable time frame (six-week experiment). Given the lack of stream connectivity for the endorheic lakes in our study area, the dispersal rates in our experiment were likely much higher than natural rates for most lakes on the Great Plains. For example, the lake on which we ran our experiment (Kenosee Lake) lacks stream connections except at high water levels (Vance et al., 1997), making direct dispersal impossible during droughts. However, it may receive dispersers transported by terrestrial animals and waterfowl that travel among the dozens of prairie pothole lakes located within 5 km of its shoreline (Hessen et al., 2019; Vanschoenwinkel et al., 2008b). We speculate that the level of dispersal among these types of prairie lakes are likely comparable to that among rock pools in Churchill, Manitoba where low (limited) dispersal rates have been documented in past studies (Ng et al., 2009; Vanschoenwinkel et al., 2008a). It is likely that the ability of dispersal to compensate for salinity-driven changes will depend both on the rate of change in salinity as well as the rate of dispersal of zooplankton among lakes on the landscape (Cottenie & De Meester, 2004). Using paleolimnological records and climate projections it is possible to model future drought conditions that will impact lake salinity levels (Fritz et al., 2000; Dai, 2012), but future studies aimed at quantifying zooplankton dispersal rates in the region are needed to fully understand the problem. Given the lack of data about zooplankton dispersal in the region, our study should be viewed as a test of the potential for dispersal to buffer zooplankton communities against salinity-driven change, rather than one that can provide a definitive answer.

Our study provides evidence that dispersal may be able to reduce structural changes in zooplankton communities impacted by climate-driven salinity change in Great Plains' lakes. Elevated salinity levels led to shifts in community composition, including reductions in cladoceran abundances relative to copepods, but these changes were muted by the immigration of individuals from surrounding lakes. In addition, our laboratory experiments showed that intraspecific variation in salinity tolerance can occur when individuals are found in lakes of differing salinities, suggesting that the ability of dispersal to compensate for salinity-driven losses may not only be a simple rescue effect, but might result from the immigration of salinity-tolerant clones from surrounding lakes. Future studies occurring over a longer time-frame would be helpful for disentangling these two mechanisms. Overall, our results correspond with those of several other studies with plankton communities that have shown the importance of dispersal for maintaining community structure and function in the face of environmental change (Cottenie & De Meester, 2004; Strecker & Arnott, 2010; Thompson & Shurin, 2012; Symons & Arnott, 2013). Given the importance of dispersal for zooplankton communities responding to a changing environment, it will be important to preserve regional biodiversity and the mechanisms and pathways that allow for dispersal of individuals among lakes and ponds on the Great Plains.

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2.8. Tables

Table 2.1. Chemical composition of salt mixture used in field experiment. The ingredients are based on the mean concentrations of elements found in lake water of the northern Great Plains (Last 1992).

Salt Parameter	**Value (g/L)**
$MgSO_4$	8.26
NaCl	18.16
$CaSO_4$-$2H_2O$	2.99
Na_2SO_4	8.52
KCl	0.4
$NaHCO_3$	2.25

Table 2.2. Chemical and physical data for Kenosee Lake and for lakes where immigrants (dispersers) were collected.

Lake	**Salinity (g/L)**	**Lake area (km^2)**	**Latitude (°N)**	**Longitude (°W)**
Kenosee	0.95	8	49.826	102.294
Big Quill	5.65	249	51.864	104.370
Peter	3.5	45	51.457	104.934
Unnamed	1.5	3	49.718	102.278

Table 2.3. ANOVA results using data collected at the end of the enclosure experiment.

	Salinity (S)		**Dispersal (D)**		**S*D**	
Metric	**F**	**P**	**F**	**P**	**F**	**P**
Abundance	1.53	0.24	0.36	0.55	1.1	0.37
Species richness	3.65	**0.03**	1.11	0.3	1.62	0.22
Diversity	0.54	0.46	0.77	0.52	3.24	0.07
Evenness	0.57	0.64	0.49	0.49	2.13	0.13
Functional richness	1.16	0.29	0.002	0.96	0.02	0.88
Functional evenness	0.68	0.57	15.2	**0.001**	4.06	**0.026**
Rao’s diversity	0.68	0.57	0.004	0.94	0.38	0.76

Table 2.4. Functional trait matrix for zooplankton found in our enclosure experiments. OC = omnivore-carnivore.

Species	**Habitat**	**Trophic group**	**Feeding strategy**	**Body length**
B. longirostris	Pelagic	Herbivore	B-filter	0.40
C. sphaericus	Littoral	Herbivore	C-filter	0.46
D. mendotae	Pelagic	Herbivore	D-filter	2.00
D. pulicaria	Pelagic	Herbivore	D-filter	1.75
D. rosea	Pelagic	Herbivore	D-filter	1.40
D. thomasi	Pelagic	OC	Raptorial	0.84
Leptodiaptomus spp.	Pelagic	Omnivore	Stationary	0.93
M. edax	Pelagic	OC	Raptorial	0.93
Ceriodaphnia spp.	Pelagic	Herbivore	D-filter	0.82
Diaphanosoma spp.	Littoral	Herbivore	S-filter	0.85
Microcyclops spp.	Pelagic	OC	Raptorial	0.59
Skistodiaptomus spp.	Pelagic	Omnivore	Stationary	1.26

Table 2.5. Information on lakes from which clones were collected for laboratory salinity tolerance experiments. Also included is the 48 h NaCl effective concentration (EC50 with 95% lower and upper confidence intervals).

Species	**Lake**	**Salinity ($g\ L^{-1}$)**	**Latitude (°N)**	**Longitude (°W)**	**48-h EC50 ($g\ L^{-1}$)**
D. pulicaria	East Stump Lake	2.99	47.520	98.212	3.70 (2.74 – 4.95)
	Devil’s Lake	1.09	48.112	98.865	1.73 (1.49 – 1.99)
C. sphaericus	Stink Lake	1.66	46.883	99.424	2.11 (1.75 – 2.55)
	Devil’s Lake	1.09	48.112	98.865	2.48 (2.01 – 3.06)

2.9. Figures

Figure 2.1. Timeline (A) and experimental design (B) of the field experiment. F-Mesocosms were filled with water and zooplankton; salt - Salt was added in intervals from day 0 to day 4; S1- first sampling date; disp- immigrants were added to enclosures assigned to the active dispersal treatment; S2- final sampling date.

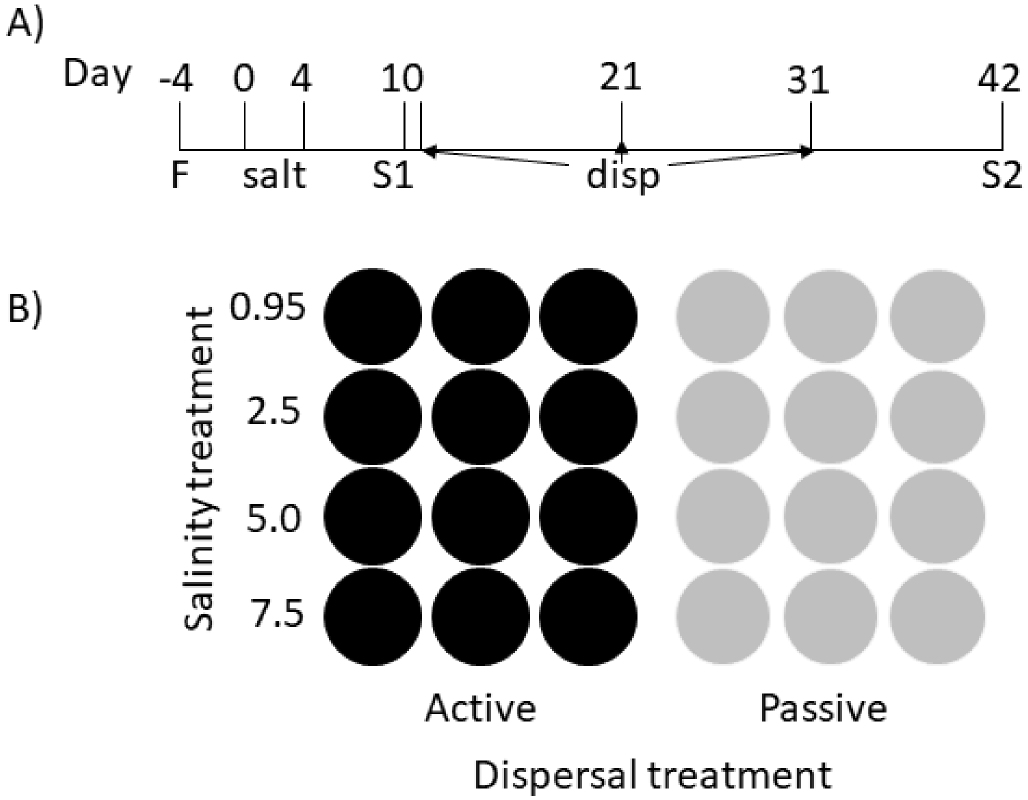


Figure 2.2. A comparison of principal component biplots based on zooplankton abundances found in enclosures at the beginning (A) and end (B) of our experiment. Each point represents a zooplankton community found in an enclosure, with darker shades representing higher salinities.

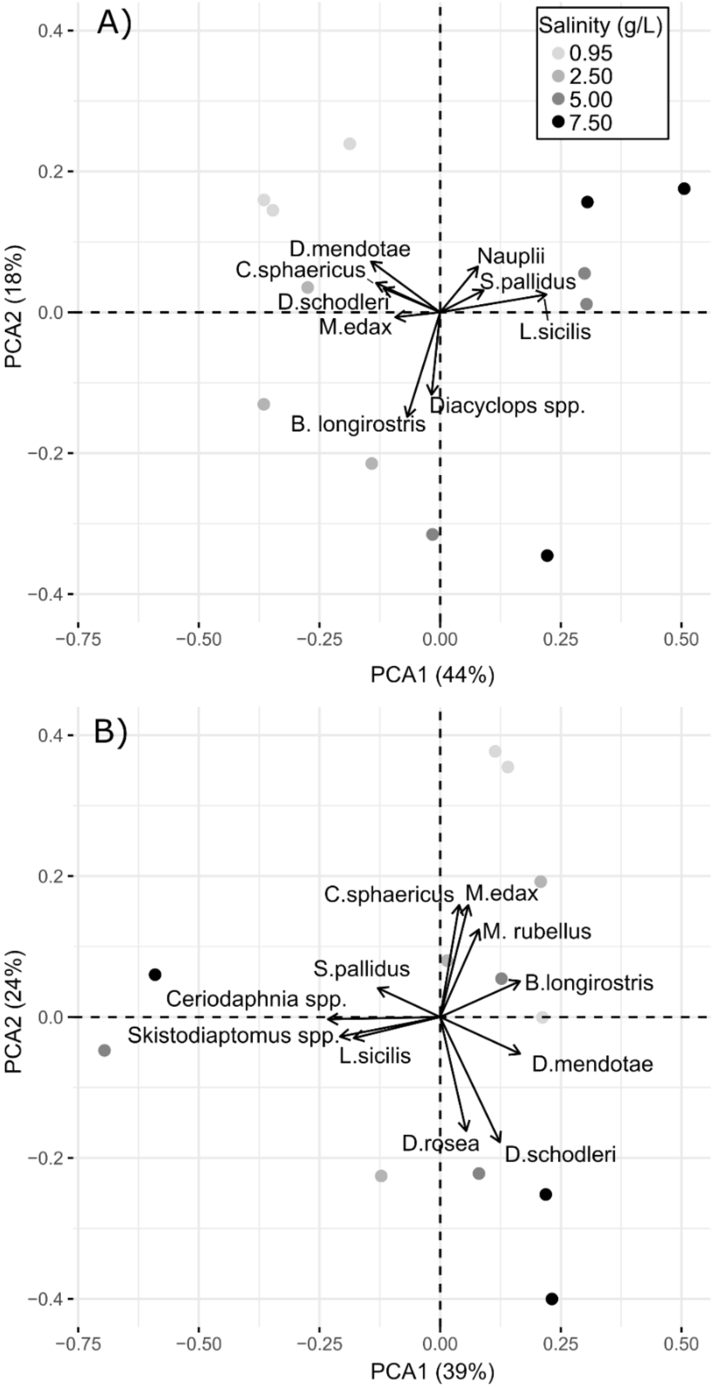


Figure 2.3. Boxplots of total abundance for cladoceran and copepod groups at the end of the experiment. Enclosures in passive dispersal treatments are located in the top panel and active dispersal enclosures are in the bottom panel.

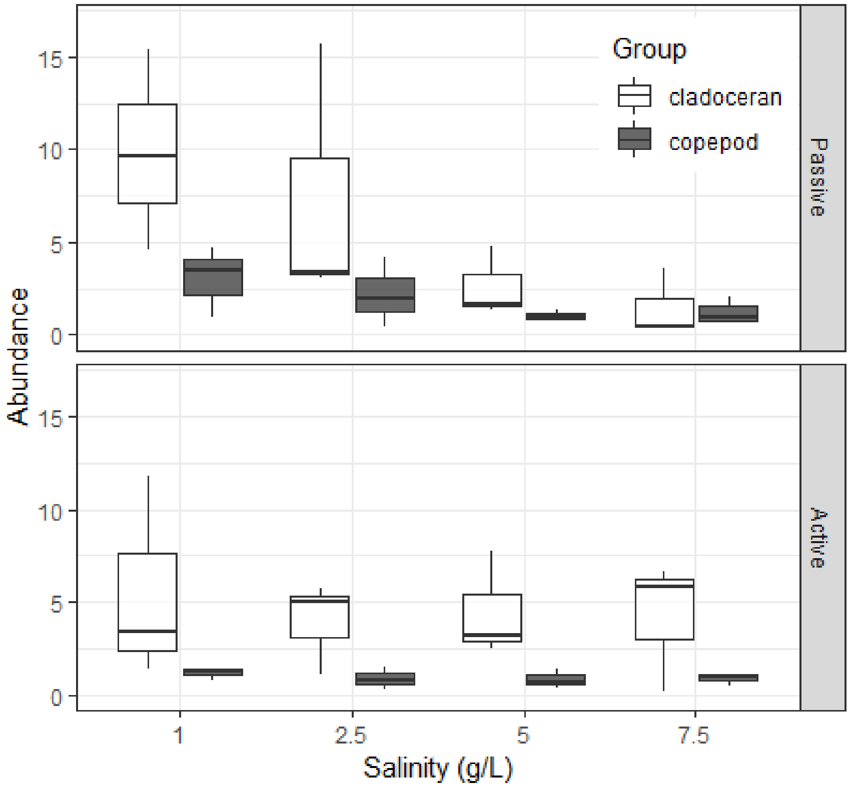


Figure 2.4. Taxonomy-based metrics of the zooplankton communities at the end of the experiment. Boxplots display total abundance (a, b), species richness (c,d), Hill diversity (e, f) and Pielou’s evenness (g, h) under eight different salinity and dispersal treatments (n = 3 each).

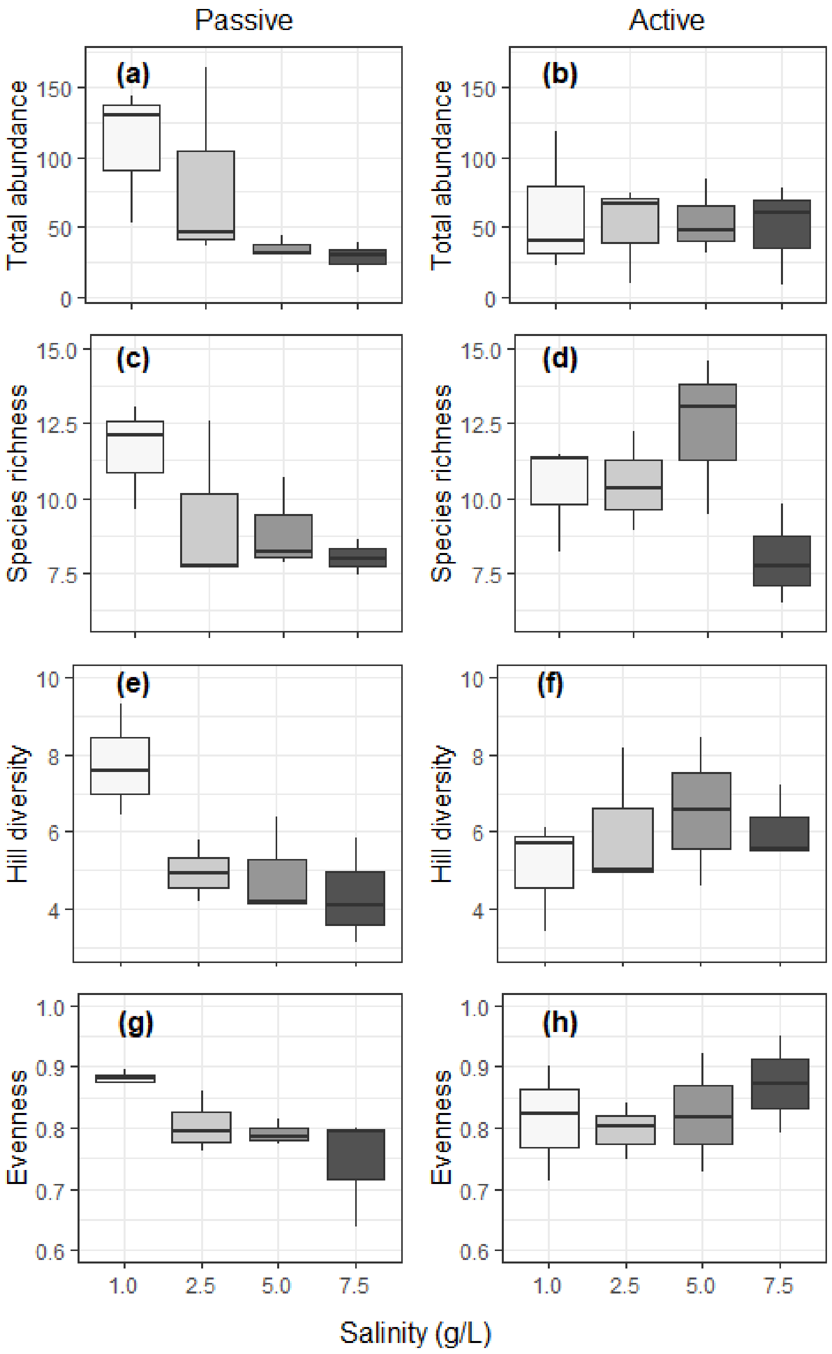


Figure 2.5. Functional metrics for zooplankton communities at the end of the six-week field experiment. Boxplots display functional richness (a,b), Rao’s diversity (c, d) and functional evenness (e, f) under eight different salinity and dispersal treatments (n = 3 each).

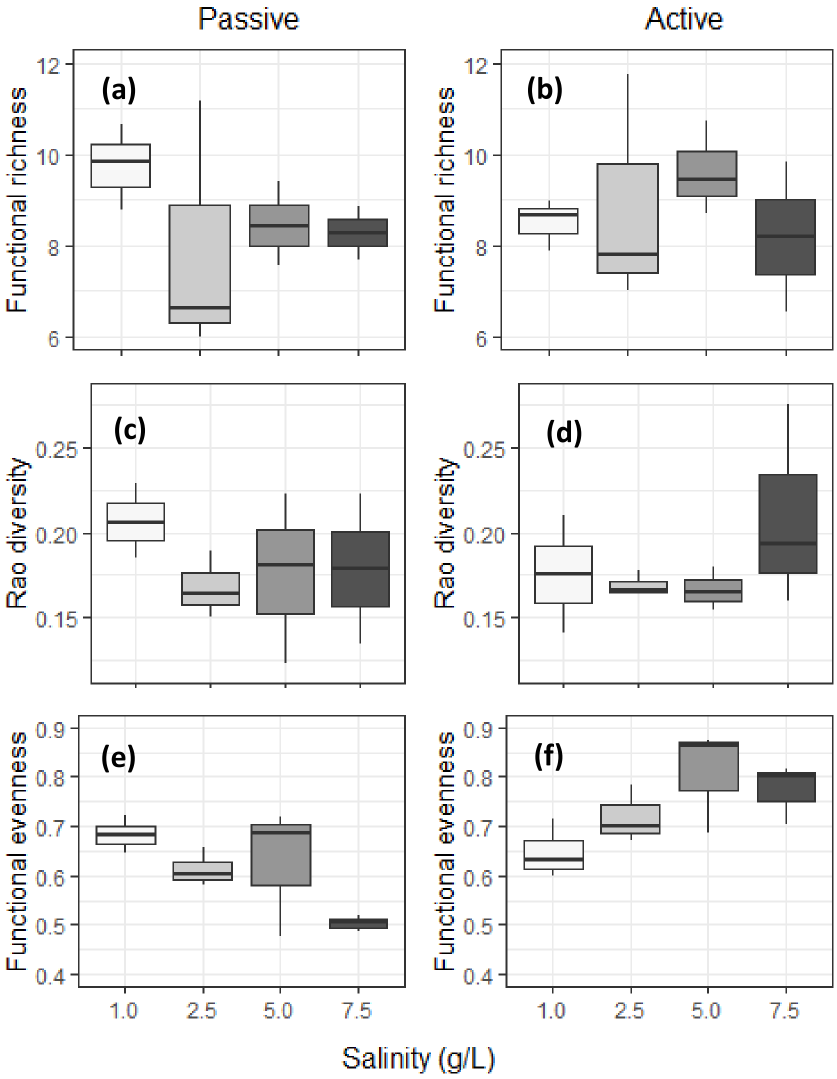


Figure 2.6. Results of a power analysis showing the statistical power available to detect differences in richness or diversity among treatments within factors (dispersal, salinity) and the interaction between dispersal and salinity.

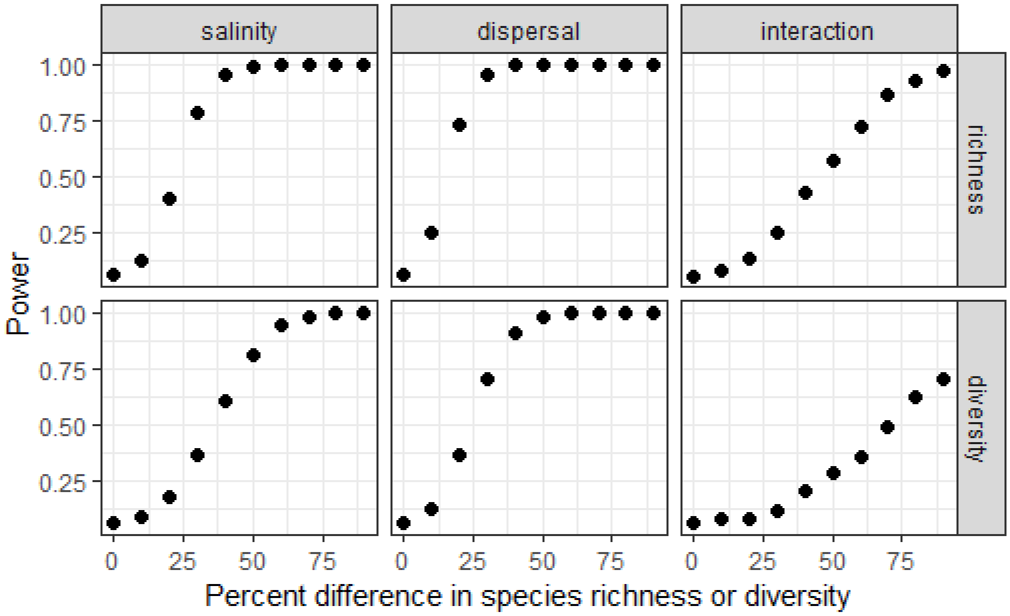


Figure 2.7. Sets of exposure-response curves based on immobility after 48 hours in response to NaCl indicating differences between (a) clones of *C. sphaericus* and; (b) clones of *D. pulicaria*.

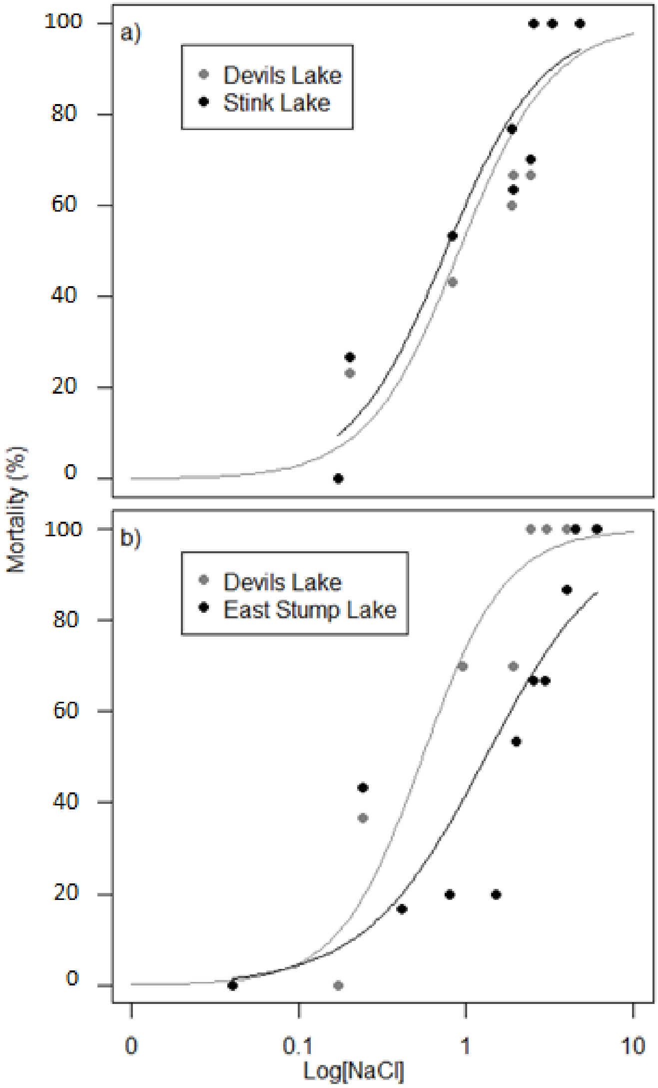
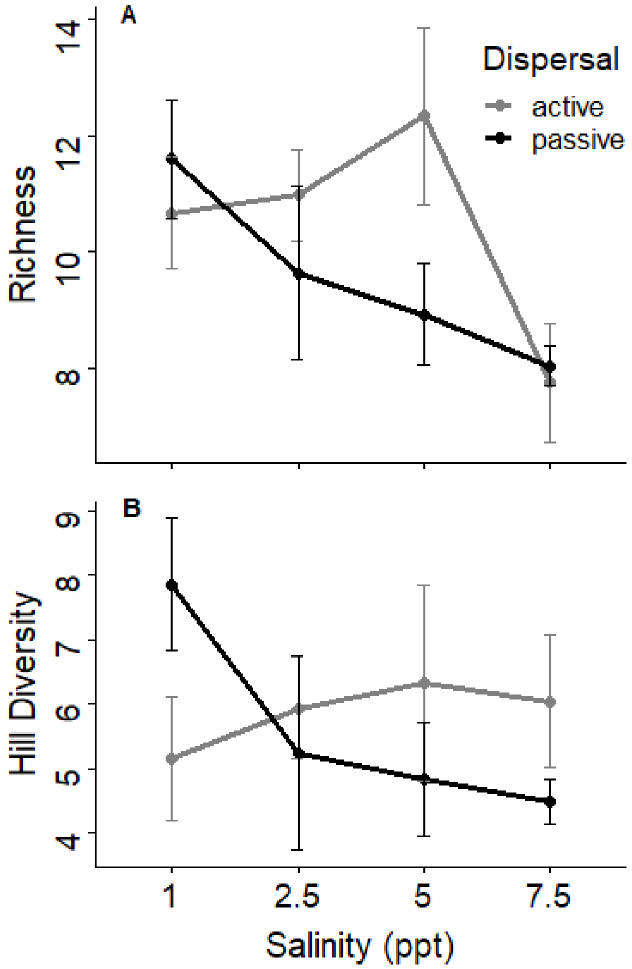


Figure S1. An interaction plot for richness (A) and diversity (B) constructed using data collected at the end of the enclosure experiment.



Chapter 3

Conclusions

3.1. Summary

This study investigated how projected salinity increases will affect freshwater zooplankton communities in the Great Plains from a metacommunity perspective. We found that experimental dispersal buffered against losses of cladocerans in communities exposed to increased salinities. Our PCAs showed that disturbed communities receiving dispersers maintained a varied abundance of cladocerans and copepods, while communities that did not receive dispersers were dominated by copepods. We proposed two mechanisms enabling dispersal-mediated compensation for lost cladocerans. The first is termed the rescue effect whereby consistent addition of cladocerans allows for sustained recolonization, thereby stabilizing communities in unfavorable habitats. The other explanation, supported by our toxicology findings, suggests dispersers could contain salinity-tolerant cladocerans due to intraspecific variation driven by adaptation to local salinity conditions. While our PCAs showed evidence of buffering by dispersal, this was not observed for univariate community diversity measures despite the reduced species richness and zooplankton abundances caused by increased salinities. Power analysis results suggested that our experiment had a relatively low power to detect such a buffering effect. Overall, simulated dispersal appeared to compensate for some changes driven by moderate salinity increases in zooplankton communities, but not others.

While the conclusions of this study provide some reasons for optimism, the true resilience of freshwater lakes in the Great Plains to salinization will depend on factors that were not directly tested in my experiments. Natural rates of dispersal among Great Plains lakes might vary dramatically depending on lake-specific factors (e.g. distance from neighbouring lakes, presence of dispersal vectors, accessibility) (Jenkins, 1995; Jenkins & Underwood, 1998; Cohen & Shurin, 2003) and may be much lower than the rate I used in my experiment. If natural dispersal rates are high enough to produce the effects found in my study, then the extent of buffering will likely depend on the real salinity differences among neighbouring lakes. Unfortunately, salinity values for lakes in southern Saskatchewan are not heterogeneous across the landscape, but are spatially autocorrelated, such that low salinity lakes are typically surrounded by others with low salinities (H. Haig, University of Regina, unpublished data). This would make it difficult for salinity-tolerant genotypes or species to access freshwater lakes that are experiencing salinization. However, there are some cases where saline lakes are found within proximity of freshwater lakes. For example, Shoe Lake (49.728N, 105.35W) is a hypersaline on the Great Plains surrounded by over a dozen smaller lakes and ponds in a 10 km^2 area that most likely have lower salinity levels (H. Haig, University of Regina, personal communication). Other factors that were not addressed in my experiments include temperature and alkalinity, which are both increasing in the region (Kaushal *et al.*, 2018). Therefore, a full understanding of the future trajectory of zooplankton communities will have to consider interactions between salinity and these other stressors that have been found to be important in past studies on zooplankton communities. Finally, my study was focused on freshwater lakes that are experiencing increased salinity levels. I did not design my study to test the potential for dispersal to buffer zooplankton communities in lakes that are currently brackish and expected to experience future salinity increases. Current distributional patterns of zooplankton suggest that there are hard limits on the upper thresholds at which most freshwater zooplankton species can survive (Wissel et al., 2011), making it unlikely that dispersal can prevent the eventual transition from a diverse freshwater zooplankton community to one that is dominated by a few salinity-tolerant species.

Based on my study, there are several lines of future inquiry that are promising. First, an important question that arises from my work is whether the effects of dispersal in my experiments were caused by source-sink population dynamics (Brown & Kodric-Brown., 1977) or the immigration of resistant clones (Weider & Hebert, 1987; Sinclair & Arnott, 2018). Longer-term experiments that involve the early introduction of dispersers followed by a long period without additional immigration would allow future studies to disentangle these two mechanisms, as source-sink dynamics rely on continuous immigration, while salinity-resistant clones should be able to persist for the entirety of the experiment. Other fruitful lines of inquiry include the quantification of dispersal rates among lakes for zooplankton on the Great Plains, the measurement of life history parameters for individual species in long-term salinity-tolerance experiments, and studies similar to mine with increased replication and higher power to detect the statistical interaction I expected to find between dispersal and salinity.

3.2. Contributions to the field

Metacommunity ecology is an approach that considers the significance of connections among communities and the role of these connections in maintaining biodiversity in the face of environmental changes such as climate-driven salinization (Heino, 2012). This study demonstrates the importance of dispersal as a regional factor in structuring zooplankton communities affected by salinity increases in the Great Plains. Although much theoretical and some experimental work has been conducted on spatial insurance (Loreau et al., 2003; France & Duffy, 2006; Gonzalez & Loreau, 2009; Thompson & Shurin, 2012; Symons & Arnott, 2013), past research had not addressed if this mechanism would operate for zooplankton communities exposed to salinity changes in regions where salinity is highly variable in space and time. My study built on previous evidence of spatial insurance operating in response to other stressors (Strecker, 2007; Staddon et al. 2010; Symons & Arnott 2013) and tested if the same process could occur for zooplankton in Great Plains lakes exposed to rising salinities. The information from my study can be used to assess how communities might change in response to climate-driven salinization and will provide a launching point for future studies that tackle questions related to natural dispersal rates and the evolution of salinity tolerance in zooplankton from this region.

3.2. How this research is integrative

Integrative biology is an interdisciplinary strategy in addressing complex scientific issues ranging from cellular studies to whole ecosystem research. This project focuses on ecological theory by nature but retains relevance to other subdisciplines in biology. The most relevant subject for my study is probably physiology, whereby the impacts of salinity on zooplankton communities begin with issues maintaining internal osmoregulatory balance. Toxicology is a branch of biology that could describe the chronic or acute effects of salinity on zooplankton at concentrations that exceed osmoregulatory capacities. One component of our study relied on toxicology to demonstrate the presence of varied salinity tolerances within zooplankton species to test if dispersal might be able to introduce tolerant clones to lakes experiencing salinization.

Lastly and most broadly, evolutionary studies were consulted and cited to provide background on the potential for zooplankton to adapt to increased salinities.

3.3. Relevance to other research

The scope of this research is related to an ongoing master's project by Mariam Elmarsafy titled, "Can Cladocera on the Great Plains of North America 'Keep Up' with Climate Change?" Her research will test if the salinity tolerance of *Daphnia* and *Ceriodaphnia* has evolved over time, and therefore will have implications for whether these species could persist in affected lakes. While my study focused on the ability of dispersal to mitigate change in salt-stressed zooplankton communities, her work is examining whether species already living in the lake can gradually adapt to changing salinities. Her findings will contribute to our knowledge about intraspecific variation in zooplankton salinity tolerance driven by local adaptation over time and could provide further evidence that variation in salinity tolerance can occur across the landscape. One of the assumptions of my work was that variation in salinity tolerance among lakes exists, so her work will be important for putting together the entire puzzle.

There is a widespread concern about how freshwater zooplankton will respond to increasing salinities as reflected in the ongoing study called the Global Salt Experiment. This project aims to investigate the impacts of road salt freshwater zooplankton ecosystems, involving twenty field enclosure experiments conducted in North America and Europe to test the long-term toxicity of sodium chloride. This study could provide comparable results regarding regional differences in zooplankton responses to salinity, as well as support my findings of reduced species richness and cladocerans as salinities increased. Both climate-driven salinity and road salt runoff are contributors to the rapid salinization of freshwaters in North America (Covich et al., 1997; Dugan et al., 2017; Kaushal et al., 2018; Schallenberg et al., 2003; Williams, 1999), and as a result, should be considered important fields to study for the management and preservation of inland aquatic ecosystems

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