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Parasite susceptibility in an amphibian host is modified by salinization and predators☆

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ABSTRACT

Secondary salinization represents a global threat to freshwater ecosystems. Salts, such as NaCl, can be toxic to freshwater organisms and may also modify the outcome of species interactions (e.g. host-parasite interactions). In nature, hosts and their parasites are embedded in complex communities where they face anthropogenic and biotic (i.e. predators) stressors that influence host-parasite interactions. As human populations grow, considering how anthropogenic and natural stressors interact to shape host-parasite interactions will become increasingly important. We conducted two experiments investigating: (1) the effects of NaCl on tadpole susceptibility to trematodes and (2) whether density- and trait-mediated effects of a parasite-predator (i.e. damselfly) and a host-predator (i.e. dragonfly), respectively, modify the effects of NaCl on susceptibility to trematode infection. In the first experiment, we exposed tadpoles to three concentrations of NaCl and measured parasite infection in tadpoles. In the second experiment, we conducted a 2 (tadpoles exposed to 0 g L^{-1} NaCl vs. 1 g L^{-1} NaCl) x 4 (no predator, free-ranging parasite-predator (damselfly), non-lethal host-predator (dragonfly kairomone), and free-ranging parasite-predator + dragonfly kairomone) factorial experiment. In the absence of predators, exposure to NaCl increased parasite infection. Of the predator treatments, NaCl only caused an increase in parasite infection in the presence of the parasite-predator. However, direct consumption of trematodes caused a reduction in overall infection in the parasite-predator treatment. In the dragonfly kairomone treatment, a reduction in tadpole movement (i.e. trematode avoidance behavior) led to an increase in overall infection. In the parasite-predator + dragonfly kairomone treatment, antagonistic effects of the parasite-predator (reduction in trematode abundance) and dragonfly kairomone (reduction in parasite avoidance behavior) resulted in intermediate parasite infection. Collectively, these findings demonstrate that NaCl can increase amphibian susceptibility to parasites, and underscores the importance of considering predator-mediated interactions in understanding how contaminants influence host-parasite interactions.

1. Introduction

Chemical contaminants represent one of the greatest current threats to aquatic ecosystems (Cañedo-Argüelles et al., 2013; Chagnon et al., 2015; Lesbarrères et al., 2014; Sasaki et al., 2015). Of particular concern is the unprecedented rate of salt accumulation in coastal and inland freshwater ecosystems (i.e. secondary salinization; Herbert et al., 2015). Salts can enter freshwater habitats through agricultural practices (i.e. irrigation water runoff), coastal flooding, and road salt application (Hill and Sadowski, 2016). Secondary salinization of freshwater systems is predicted to continue increasing over time because unlike some contaminants that degrade rapidly, the high environmental stability of salts result in their accumulation within water and soil (Herbert et al., 2015). Therefore, understanding the ecological consequences of salinization is critical to protecting our freshwater ecosystems.

Salinization of freshwater systems can result in both direct and indirect effects on aquatic organisms. Single-species toxicity assays have demonstrated that salt concentrations commonly found in nature are directly toxic to a number of freshwater species (Sanzo and Hecnar, 2006; Karraker et al. 2008; Mahrosh et al., 2014; Searle et al., 2016). For example, Collins and Russell (2009) found that Cl^{-} concentrations that are commonly found in roadside

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wetlands ($0.3–6.1\ g\ L^{-1}$) caused mortality across five common North American amphibian species. In addition to the direct toxic effects of salt on individual organisms, increased salinization can negatively affect aquatic organisms via indirect pathways. Using low, environmentally-relevant concentrations of NaCl, Hintz et al. (2016) found that NaCl caused a reduction in the density of zooplankton, resulting in a direct positive effect of salinity on phytoplankton abundance. This increase in phytoplankton abundance ultimately resulted in a trophic cascade that lowered the biomass of filamentous algae. As secondary salinization continues to threaten freshwater systems, studies evaluating both the direct and indirect effects of salt on species interactions will be critical for understanding the mechanisms that shape species abundance and diversity.

The effect of contaminants on the interaction between hosts and their parasites has received significant recent attention (Gustafson, 2016; Sures et al., 2017). Environmental contaminants can mediate host-parasite interactions via several mechanisms. For example, contaminants can influence host-parasite interactions directly by reducing the abundance of either parasite or host (Rohr et al. 2008a,b) or by altering their respective traits, such as infectivity of the parasite, immune response of the host, behavior of the parasite, or behavior of the host (Christin et al., 2003; Rohr et al. 2008a,b; Denoël et al., 2013). Despite the influence that contaminants may have on host-parasite interactions, relatively few studies have investigated the consequences of salinization on disease outcomes (Hall et al., 2013; Milotic et al., 2017; Studer and Poulin, 2012). Additionally, salinization can often occur at relatively low concentrations ($\leq 1\ g\ L^{-1}$ NaCl; Milotic et al., 2017). While these low concentrations of salt may not cause direct mortality (Gonçalves et al., 2007; Collins and Russell, 2009), it is imperative to consider the potential indirect effects that these low concentrations may have on host-parasite interactions.

Finally, in nature, hosts and their parasites are embedded in complex ecological communities where they interact with other species that can also contribute to the effects of contaminants on disease outcomes. For instance, the presence of predators can directly alter infection outcomes by reducing abundance of the parasite or host (a density-mediated effect; Ostfeld and Holt, 2004; Orlofske et al., 2014), as well as influence infection outcomes by altering the behavior of hosts, such as those that are associated with parasite avoidance. For example, in the presence of trematodes, tadpoles commonly display heightened activity levels to avoid trematode infection (Daly and Johnson, 2011). However, in the presence of both predators and trematodes, tadpoles have been shown to reduce their activity levels to avoid predation, leading to an increase in trematode infection (a trait-mediated effect; Thiemann and Wassersug, 2000; Orlofske et al., 2014). Despite the potential role that other species (i.e. predators) in the community may play in shaping disease outcome, most studies investigating the effects of contaminants on host-parasite outcomes are conducted in isolation of other species interactions (Koprivnikar et al., 2007; Rohr et al. 2008a,b; Studer and Poulin, 2012; Milotic et al., 2017). Hosts and their parasites encounter both abiotic (i.e. contaminants) and biotic factors (i.e. predators) within their natural environment. Therefore, to better understand how contaminants affect host-parasite outcomes, there is a need to consider the added complexity of interactions between multiple factors.

Towards this goal, an amphibian-trematode model is an excellent system for testing the interaction of salinization and predators on host-parasite interactions. Many have hypothesized that contaminants play a significant role in shaping disease outcomes of amphibians (Collinge and Ray, 2006; Rohr et al. 2008a,b). Indeed, previous work demonstrates that both amphibians and cercariae, a free-swimming stage in the trematode life cycle, are susceptible to environmental contaminants (i.e. pesticides) at ecologically-relevant concentrations (Rohr et al. 2008a,b; Hua et al., 2016). Further, this system is also ideal because past work has shown that contaminants and predators can both independently mediate infection outcomes in host-parasite interactions (Rohr et al. 2008a,b, 2015, Orlofske et al., 2012, 2014, Groner and Relyea, 2015). Therefore, using the amphibian-trematode model, this study aimed to: 1) Determine the effects of increased salinity on tadpole susceptibility to trematode infection 2) Investigate whether density-mediated effects of a parasite-predator and trait-mediated effect of a non-lethal host-predator can modify the effects of increased salinity on infection outcomes.

2. Materials and methods

2.1. Study system

To address these goals, we chose to work with environmentally-relevant concentrations of NaCl. NaCl is a ubiquitous wetland contaminant which can enter freshwater systems in a variety of ways. In northern latitudes, NaCl is found within freshwater largely as a result of road deicer runoff (Evans and Frick, 2001; Kelly et al., 2010). Chloride concentrations associated with road de-icing have been shown to range from $0.150\ g\ L^{-1}$ in rural lakes to as high as $5\ g\ L^{-1}$ in more urban lakes and wetlands (Evans and Frick, 2001). Further, NaCl can also enter wetlands through the clearing of natural vegetation for agriculture by reducing buffer zones between roadways and wetlands (Barica, 1972). Other agricultural practices such as crop irrigation can also increase wetland salinization, as water used to irrigate crops often contains naturally occurring salts (Ghassemi et al., 1995). Chloride concentrations in ground water near agricultural areas can be as high as $46\ g\ L^{-1}$ due to these irrigation practices, and can then leach or runoff into nearby bodies of water (Herbert et al., 2015).

For the parasite, we chose to work with echinostomes, a family of digenetic trematodes. Trematodes have complex life cycles, with snails and bivalves serving as the first intermediate host, amphibian larvae as the second intermediate host, and birds or mammals serving as definitive hosts (Huffman and Fried, 2012). As the first intermediate host, snails are penetrated by miracidia in the head-foot region, which forms a sporocyst (Kanev et al., 2000). Sporocysts then produce rediae, which form free-living cercariae. These cercariae leave the snail, infect amphibian tadpoles, and then encyst in the kidneys of the tadpole forming metacercariae. Amphibian hosts are consumed by bird or mammalian predators, where the parasite sexually reproduces within the gut of the bird or mammalian host. The parasites then return to the aquatic environment via eggs embedded in the feces of the bird or mammalian host. Trematode infections are the most common parasite infection reported across several amphibian species, with mortality and pathology of amphibian hosts being dose-dependent (increasing with total number of metacercariae within the host; Holland et al., 2007). We utilized the cercarial stage of the trematode, as it is one of the stages that is most likely to be directly exposed to NaCl within wetlands. This free-living cercariae stage also serves a vital role as a prey species within several aquatic food webs (Johnson et al., 2010; Lafferty et al., 2006).

For the host, we chose to work with wood frog tadpoles (*Lithobates sylvaticus*). Wood frogs are one of the most widely distributed amphibian species (Conant and Collins, 1998) and often occur in bodies of water that are located near roadways where they may be exposed to NaCl (Sanzo and Hecnar, 2006; Karraker et al. 2008). Additionally, they have been shown to be susceptible to both NaCl ($LC50_{96} = 5.11\ g\ L^{-1}$ NaCl; Sanzo and Hecnar, 2006) and to parasite infection (Rohr et al. 2008a,b; Pochini and Hoverman, 2017).