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Thermal variation and factors influencing vertical migration behavior in *Daphnia* populations

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ABSTRACT

The antipredator behavior diel vertical migration (DVM), common in aquatic keystone species *Daphnia,* involves daily migration from warmer surface waters before dawn to cooler deeper waters after dusk. Plasticity in *Daphnia* DVM behavior optimizes fitness via trade-offs between growth, reproduction, and predator avoidance. Migration behavior is affected by co-varying biotic and abiotic factors, including light, predator cues, and anthropogenic stressors making it difficult to determine each factor's individual contribution to the variation in this behavior. This study aims to better understand this ecologically significant behavior in *Daphnia* by: (1) determining how *Daphnia pulicaria* thermal preferences vary within and among natural populations; (2) distinguishing the role of temperature verses depth in *Daphnia* vertical migration; and (3) defining how two anthropogenic stressors (copper and nickel) impact *Daphnia* migratory behavior.

Simulated natural lake stratification were constructed in 8 L (0.5 m tall, 14.5 cm wide) water columns to monitor under controlled laboratory conditions the individual effects of temperature gradients, depth, and metal stressors on *Daphnia* vertical migration. Three major findings are reported. First, while no difference in thermal preference was found among the four populations studied, within lake populations variability among isolates was high. Second, decoupling temperature and depth revealed that depth was a better predictor of *Daphnia* migratory patterns over temperature. Third, exposure to environmentally relevant concentrations of copper or nickel inhibited classic DVM behavior. These findings revealed the high variability in thermal preference found within *Daphnia* populations, elucidated the individual roles that depth and temperature have on migratory behavior, and showed how copper and nickel can interfere with the natural response of *Daphnia* to fish predator cues. Thus contributing to the body of knowledge necessary to predict how natural populations of *Daphnia* will be affected by climate related changes in lake temperatures and increased presence of anthropogenic stressors.

1. Introduction

The micro-crustacean zooplankton genus *Daphnia* are ubiquitous in the world's lentic (e.g., lake and pond) ecosystems (Shaw et al., 2007), and are an integral component of aquatic food webs (i.e., keystone species) due to their central role in transferring the biomass of primary producer's (e.g. algae) up the food chain by being the primary food for smaller fish (Colbourne et al., 2004; Sarnelle, 2005). *Daphnia's* pervasiveness is due in part to their ability to tolerate a dynamic range of environmental conditions, in particular temperature. *Daphnia* migrate within the water column on a daily basis to avoid predation, a behavior called diel vertical migration (DVM), which exposes them to a wide range of temperatures (Gliwicz, 1986; Lampert, 1989, 1993; Loose, 1993). Additionally, avoidance of inter- and intraspecific competition has also been linked to distinct patterns of *Daphnia* distribution within the water column (De Meester and Dumont, 1988; 1989; Dumont et al., 1985; Weider, 1984). As surface water temperatures continue to increase as a result of climate change, even large lentic systems such as the Great Lakes are predicted to become more variable, leading to changes in vertical mixing and the degree to which lakes will thermally stratify (Kling et al., 2003; McCormick, 1990; Snucins and Gunn, 2000; Thuiller, 2007; van de Waal et al., 2009). Thermal stratification in lakes results from seasonal climatic patterns which produce distinct thermal layers that decrease in temperature with depth (Wetzel, 2001), creating thermal niches. Thermal stratification not only influences the distribution of

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aquatic organisms, based on thermal optimums and ranges, but predator-prey dynamics as well (Wetzel, 2001). Therefore, changes in lake stratification are likely to impact the distribution and fitness of aquatic organisms such as *Daphnia*, which are heavily influenced by temperature (Heino et al., 2009; Mooij et al., 2005), thereby effecting ecosystem function due to their central role in aqu“atic ecosystems (Mooij et al., 2005; Thuiller, 2007; van de Waal et al., 2009).

Classic DVM behavior in *Daphnia* is a migration to deeper, darker, and cooler waters during the day to avoid visual predators and a migration to warmer surface waters during the night to feed when the risk of predation is reduced (Gliwicz, 1986; Lampert, 1989, 1993; Loose, 1993; Sitch, 1989). This negative photo-taxis behavior is triggered by a combination of light and predatory (i.e., kairomone) cues (Dawidowicz and Loose, 1992; Lampert, 1989, 1993; Loose, 1993). In the absence of light or predator cues, *Daphnia* remain in the warmer and food-rich surface waters which has been shown to lead to increased growth and reproduction rates in *Daphnia* (Dawidowicz and Loose, 1992; Lampert, 1989, 1993; Loose, 1993). Thus, indicating a fitness costs associated with DVM.

Lampert (1989) described three potential sources of fitness cost associated with diel vertical migration: 1) differences in food quality and quantity, 2) distance of migration (i.e., changes in depth), and 3) changes in temperature. The cost associated with food quality and quantity depends mainly on the assumption that algae is primarily found in the surface waters of the euphotic zone (Gliwicz, 1986; Lampert, 1989, 1993; Loose, 1993; Sitch, 1989); however, recent studies have shown that high levels of algal biomass can exist outside the euphotic zone (Winder et al., 2003). Thus, putting into question the validity of the assumption that food availability is a true cost associated with DVM. While the effects of migration depth and temperature on *Daphnia* fitness have been well documented (e.g., Dawidowicz and Loose, 1992; Lampert, 1989, 1993; Loose, 1993), how these two factors independently influence the distance *Daphnia* migrate, in the presence of light and predator cues, is far less understood. This is because light, temperature, and depth are all naturally coupled (Loose and Dawidowicz, 1994; Lampert, 1989, 1993; Loose, 1993).

A cost associated with DVM not addressed in Lampert's (1989) paper is the disruptive effect chemical stressors, such as metals, can have on *Daphnia* migration patterns. Globally, metals are deposited in lakes through natural processes. However, over the past century elevated levels of metals are being loaded into lakes by anthropogenic activities resulting in potentially irreversible impacts on aquatic organisms and the ecosystems as a whole (Gunn et al., 1995; Keller, 2009; Keller et al., 1992; Keller and Piblado, 1986; Pyle et al., 2005). Studies have shown that metals in aquatic environments can cause physiological stress and impair behavioral and ecological activities (Atchison et al., 1987; Scott and Sloman, 2004). In *Daphnia*, environmentally relevant levels of Cu and Ni have been shown to disrupt their ability to detect the kairomone cue of predators, such as the *Chaoborus*, an invertebrate predator, and preventing the induction of defensive neckteeth on *Daphnia* (Hunter and Pyle, 2004; Mirza and Pyle, 2009). However, little is known about how kairomones of vertebrate predator, such as fish, and metals interact to influence thermal preferences associated with diel vertical migration of *Daphnia*. Furthermore, few if any studies have characterized the individual variation in thermal preferences within and among natural populations of *Daphnia*, to elucidate the environmental plasticity of the DVM behavior. Given the fitness consequences of DVM, it is critical to understand how genetic variation, biotic factors and abiotic factors contribute to phenotypic variation. Therefore, the goals of this study were to: (1) determine the thermal distribution of *Daphnia* isolates within and among natural lake populations; (2) elucidate the influence of depth and temperature variation on vertical migration behavior of *Daphnia* isolates; and (3) determine the impact of Cu and Ni on the vertical migration of *Daphnia* isolates with different thermal ranges, in the presence and absence of classic DVM conditions.

2. Materials and methods

2.1. Experimental populations

All *Daphnia pulicaria* isolates used in this study were collected from lakes in the Canadian Shield region of Ontario, Canada. Three lakes located in Sudbury, Ontario, Canada (Joe: 46° 44″–81° 31″, MacFarlane: 46° 25″–80° 59″, and Simon: 46° 23″–81° 11″) and one lake in Dorset, Ontario, Canada (Brandy Lake: 45° 06″–79° 31″). The lakes differ in their physiological and chemical attributes (Table 1). *Daphnia* from these lakes were genotyped to determine genetically distinct isolates, while being maintained for five years prior to conducting these studies under standard laboratory conditions (i.e., 20 °C, 16:8 h light: dark cycle) as described in Shaw et al., (2006). Only adult *Daphnia*, defined as those with embryos in their brood chamber, were used since adult *Daphnia* are susceptible to predation by fish and are more likely to exhibit migratory behavior responds to avoid predation (Lampert, 1993, 2006).

2.2. Experimental water columns

Experiments were conducted in one of eight glass columns (0.5 m tall, 14.5 cm diameter) filled with 8 L of the artificial lake media COMBO (Kilham et al., 1998; Fig. 1). To isolate the effects of depth and temperature on *Daphnia* vertical migration behavior we conducted laboratory experiments that decoupled these two naturally co-varying factors while controlling for other factors known to vary with depth in natural lakes to avoid confounding results. These controlled factors included light and predator cue levels, as well as food availability. The influence of food availability on diel vertical migration is unclear, due to the recent finding that algal biomass can be present outside the euphotic zone (Winder et al., 2003); therefore, we did not include food availability in our experimental design. The light sources were set-up to prevent any variation in light levels throughout the experimental water columns, with measurements taken throughout the water column on all eight columns before each experiment and showing no variation in light levels within and among water columns for any of the experiments (data not shown). The constant light levels throughout the experimental water column prevented any refuge, allowing the *Daphnia* to experience constant diel vertical migration behavior inducing conditions throughout the water column. The thermally stratified water column, constant level of light throughout the water column, control over the presence of kairomone, and the decoupling of temperature and depth (see Fig. 1) in our experimental design enabled us to examine the individual role temperature and depth play in determining the vertical migration response in *Daphnia* in a stratified system.

The thermal gradient was established by placing the water

Table 1
Physical and chemical properties associated with the four study lakes (Girard et al., 2007; L.W.Q.P., 2004).

Lake	Size (ha)	Volume (10^4 m^3)	Max depth (m)	pH	Trophic status
Brandy	108	378	7.5	6.75	Oligotrophic
Joe	180	2012	34	6.60	Oligotrophic
MacFarlane	166	2990	18	7.53	Mesotrophic
Simon	102	1224	12	7.69	Eutrophic