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An examination of UV radiation tolerance and photoenzymatic repair capabilities across temperature in the freshwater cladocerans *Scapholeberis mucronata, Diaphanosoma birgei,* and *Moina* spp

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ABSTRACT

Ultraviolet (UV) radiation has multiple consequences to freshwater organisms. Some zooplanktons use photoenzymatic repair (PER), which is a process that utilizes ultraviolet-A and visible light (photorepair radiation, PRR) to repair ultraviolet-B-induced DNA damage. Some zooplanktons also repair damage via nucleotide excision repair (NER), which is a radiation-independent enzymatic process. Our objective was to determine the effects of UV radiation, including the use of PER and NER on the cladocerans *Diaphanosoma birgei, Scapholeberis mucronata*, and *Moina* spp. Based on studies with *Daphnia*, we hypothesized that the use of PER and NER varies with temperature and across species. The three taxa were exposed to UV-B radiation followed by photorepair radiation (+PRR) or no photorepair radiation (−PRR). The occurrences of PER and NER were determined indirectly by monitoring the survival and reproduction after exposure. Experiments were performed at 10, 15, 20, 25, and 30 °C. *S. mucronata* and *Moina* spp. use PER effectively at all temperatures, whereas *D. birgei* uses PER less effectively and only at warmer temperatures. *S. mucronata* and *Moina* spp. use NER more effectively at colder temperatures, while *D. birgei* uses little to no NER. These findings have implications on how these organisms may adapt to changing UV and thermal conditions.

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PER; photoenzymatic repair; ultraviolet radiation; *Scapholeberis*; *Moina*; *Diaphanosoma*; temperature

Introduction

Climate change continues to be a threat to aquatic ecosystems throughout the world, resulting in increased water surface temperatures and enhanced thermal stratification (Häder et al. 2015). The effects of ultraviolet (UV) radiation on aquatic organisms in the context of climate change may be beneficial or detrimental, depending on the complex interactions between multiple environmental factors (Williamson et al. 2014). These factors include stratospheric ozone, which influences ambient UV; chromophoric dissolved organic matter, which influences underwater UV transparency; and temperature, which can influence organisms' response to UV (Williamson et al. 2014).

Ultraviolet-B (UV-B) radiation contains enough energy to damage an organism's DNA by forming dimers (the linkage of adjacent pyrimidine nucleotide bases), which can lead to cell death if not repaired. Some species of freshwater zooplanktons have adaptions that allow them to better withstand UV-B radiation, including photoenzymatic repair (PER), a mechanism in which visible

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light and ultraviolet-A (UV-A) radiation (collectively referred to as photorepair radiation or PRR) undo damage done by UV-B radiation. PRR activates a photoreactivating enzyme, photolyase, which creates a bridge to heal the dimer, allowing the organism to survive otherwise-deadly DNA mutations (MacFadyen et al. 2004). In the absence of PRR, organisms may also repair UV damage using the multi-enzymatic process of nucleotide excision repair (NER), which does not require light and hence is often called dark repair (MacFadyen et al. 2004). Protective compounds such as carotenoid pigments and mycosporine-like amino acids can also buffer against UV-induced DNA damage in the absence of PRR, a strategy referred to as photoprotection (Hansson and Hylander 2009).

The use of PER, NER, and photoprotection in freshwater zooplanktons varies across species. Additionally, consistent with the enzyme kinetics theory, the effectiveness of PER and NER varies with temperature. Species that are known to rely on PER (*Daphnia catawba* and *Leptodiaptomus minutus*) show higher UV tolerance at elevated temperatures, whereas species that do not use PER (*Asplanchna girodi*) are less UV-tolerant at elevated temperatures (Williamson et al. 2002). Consistent with these findings, MacFadyen et al. (2004) found an increase in PER effectiveness at higher temperatures (25 vs. 15 °C) in *Daphnia pulicaria*. In contrast, Connelly et al. (2009) observed increased PER effectiveness at colder temperatures (10 vs. 20 °C) in *D. pulicaria* and three other *Daphnia* species. Of the four *Daphnia* species, only *Daphnia pulex* used NER and did so only at 10 °C (Connelly et al. 2009), whereas MacFadyen et al. (2004) found greater use of NER compared to PER in *D. pulicaria* and no significant effect of temperature on NER.

The use of repair mechanisms and their temperature dependence is well studied within the *Daphnia* genus, but there are many common, widely distributed freshwater zooplankton taxa for which the UV-coping strategies are not well known. For example, *Moina* spp. is found throughout the world, excluding cold-temperate regions (Goulden 1968), but little is known about its responses to UV, with a few exceptions (e.g. Ramos-Jiliberto et al. 2004). Similarly, *Diaphanosoma* spp. is a cosmopolitan genus (e.g. Korovchinsky 1986) and its abundance can exceed that of *Daphnia* as the dominant cladoceran in water-supply reservoirs in central North Carolina, USA (S.L. Cooke, unpublished data). Limited UV research on *Diaphanosoma* spp. includes evidence of downward migration in response to UV (Boeing et al. 2004) and evidence of a Chilean species using PER and being highly UV-sensitive (Ramos-Jiliberto et al. 2004). However, contrary to *Daphnia*, a North American *Diaphanosoma* population showed no survival differences when incubated in UV-exposed and UV-shielded enclosures in a transparent lake (Williamson et al. 1994). Finally, *Scapholeberis* spp. is found in littoral habitats throughout the northern hemisphere (Davidson et al. 1998), often feeding at the water surface, which may explain why most *Scapholeberis* populations are highly pigmented (Cooke et al. 2015). Hurtubise et al. (1998) found *Scapholeberis kingii* to be highly UV-sensitive, despite being darkly pigmented, but to our knowledge, this is one of the only published studies of UV effects on *Scapholeberis*.

The goal of this study was to compare the responses of *Scapholeberis* spp., *Moina* spp., and *Diaphanosoma* spp. to UV-B radiation exposure. Specifically, our objectives were to determine: (1) if each species uses PER and whether temperature has an effect on this mechanism, and (2) the UV sensitivity of each species in the absence of PRR (indicative of dark repair and photoprotection) and whether temperature has an effect on these strategies collectively. We conducted a series of UV exposure experiments in temperature-controlled chambers at 10, 15, 20, 25, and 30 °C to test our hypothesis that these cladocerans' responses to UV will vary across temperature.

Methods

Zooplankton collection and lab-rearing

Scapholeberis mucronata and *Diaphanosoma birgei* were collected from City Lake, a shallow (mean depth = 4.9 m), turbid (Secchi depth < 1 m), eutrophic (Touchette et al. 2007) impoundment

located in Jamestown, North Carolina, USA (35.99° N, 79.95° W). *Moina* spp. were obtained from Carolina Biological Supply Company (Burlington, North Carolina, USA). All species were raised in City Lake water in an environmental chamber (Percival Scientific, Perry, Iowa, USA) set at 22 °C and a 14:10 light:dark cycle. The zooplanktons were fed *Nannochloropsis* algae *ad libitum* (Carolina Biological Supply Company, Burlington, North Carolina, USA). *S. mucronata* and *Moina* were maintained for several generations (i.e. several days to two weeks) prior to being used in the experiments, but *D. birgei* was used within a few days of collection due to their general sensitivity to laboratory conditions.

Experimental design and exposure conditions

The experimental design was similar to other studies that have examined the effects of temperature on PER in freshwater zooplanktons (e.g. Connelly et al. 2009). The experiment consisted of three treatments: a zooplankton group exposed to an acute dose of UV-B radiation followed by +PRR, a group exposed to an acute dose of UV-B radiation followed by dark conditions (i.e. no photorepair radiation; −PRR), and a dark control group. Each treatment consisted of four replicate dishes, each containing 10 individual organisms. Our response variable was zooplankton survival post-exposure. Although we did not directly measure DNA damage and repair, differences in survival among such exposure conditions are often used as an indicator of PER in similar experiments (e.g. Grad et al. 2001; Ramos-Jiliberto et al. 2004) and Connelly et al. (2009) found that survival correlates well with DNA repair capacity.

Experiments were conducted in an environmental chamber (Percival Scientific, Perry, Iowa, USA) at five different temperatures: 10, 15, 20, 25, and 30 °C. UV-B exposure was administered by a Spectroline XX15B 312 nm UV-B lamp (Spectronics Corporation, Westbury, New York, USA) suspended 24 cm above the dishes of organisms. This is the same lamp model used by Williamson et al. (2001) and subsequent studies by this research group (e.g. MacFadyen et al. 2004) and by Connelly et al. (2009). Similar to Connelly et al. (2009), we exposed the zooplankton to UV-B for only 15 minutes. Substantial DNA damage induction can occur in such a small exposure time because the lamp's spectral output extends into the UV-C (Connelly et al. 2009). The lamp was turned on for at least one hour prior to the experiment to warm-up to full output capacity. PRR was administered immediately following UV-B exposure for 24 hours using a Spectroline XX15N 365 nm UV-A lamp (Spectronics Corporation, Westbury, New York, USA), four 32 W cool white bulbs, and two 17 W cool white bulbs (Philips, Amsterdam, Netherlands). The four 32 W bulbs were aligned vertically in each of the chamber's corners and the two 17 W bulbs and UV-A lamp were suspended horizontally 24 cm above the organisms with the UV-A lamp in between the 17 W bulbs. However, due to a malfunction with the UV-A lamp, the 10 and 20 °C experiments with *D. birgei* and *S. mucronata* and all experiments with *Moina* spp. did not receive UV-A as part of the PRR treatment.

Experimental procedures

Experiments for *D. birgei* and *S. mucronata* were run concurrently at each temperature over a period of several weeks (June and July 2016), while *Moina* experiments were conducted later (September to December 2016). Before each experiment, organisms were acclimated to the desired temperature for approximately 72 hours in the environmental chamber, which was set on a 14:10 hour light:dark cycle. Algal food and lake-water sources were also acclimated prior to the experiment.

Immediately prior to each experiment, organisms were placed in shallow (15 mm deep × 60 mm diameter) Pyrex dishes, of which the outer edges were wrapped in black electrical tape to limit the amount of radiation scattering and to ensure more uniform UV-B and PRR exposure across replicates. Each Pyrex dish was filled with approximately 15 mL Whatman GF/F filtered City Lake water. For *D. birgei*, the dishes were filled to the very top and a pliable Aclar plastic disk (type PCTFE

P4000TR; Honeywell International, Pottsville, Pennsylvania, USA) was placed on top, taking care to remove all air bubbles because this species was prone to getting stuck in the air–water interface. Aclar is transparent to all photosynthetically active radiation (400–700 nm), UV-A, UV-B, and most UV-C, with a sharp wavelength cut-off and 50% transmission at 212 nm (Cooke et al. 2015). For *S. mucronata* and *Moina*, no cover was placed over the dishes for the exposure periods.

The control group was placed in a dark foil-covered box to ensure no exposure and the box was placed on a shelf above the UV-B lamp in the environmental chamber. Both PRR groups were placed directly under the UV-B lamp, alternating the placement of the +PRR and −PRR dishes. After the 15-minute exposure period, the +PRR group was kept on the same central shelf, centered directly under the UV-A lamp and in between the two horizontal cool white lamps, and exposed to PRR for 24 hours, while the −PRR group was placed in the box with the dark controls. After 24 hours, all lamps were turned off and all dishes were maintained in the dark for the remainder of the experiment. Survival and neonate production were observed at 0, 24, 48, and 72 hours after the 24-hour PRR exposure period. Dead individuals were removed, but neonates were kept in the dishes. For *Moina* and *S. mucronata*, it was often difficult to distinguish between neonates and the original adults due to the rapid generation times and growth rates of these species, and so the total number of living individuals was recorded as 'percent survival and reproduction' for each species. Each replicate received 0.5 mL of algal food source each time survival and reproduction were observed.

Data analysis

To determine if there were significant differences between the +PRR, −PRR, and the dark control over time post-exposure, we used repeated measures analysis of variance. Percent survival and reproduction data were log-transformed (log $(n + 1)$) to achieve normality. We used the Huynh–Feldt adjusted F statistic for determining the significance of time × treatment interactions (Von Ende 2001). Analyses were performed using IBM SPSS Statistics Version 24.

Results

At all temperatures, *S. mucronata* survival and reproduction were lowest in the −PRR (Figure 1, Table 1) and did not significantly differ between the +PRR and dark control ($p > 0.05$ for all temperatures), indicating that this species uses PER, but that PER is not temperature-dependent. Although survival and reproduction in the +PRR at 25 and 30 °C appeared lower than the dark controls, *post hoc* analyses indicated that the differences were not significant ($p = 0.762$ for 25 °C; $p = 0.877$ for 30 °C). In contrast to PER, dark repair and photoprotection in *S. mucronata* appear to be temperature-dependent, as indicated by their survival and reproduction in the −PRR across temperatures (Figure 1). Survival in the −PRR was significantly higher at 10 °C than it was at 15 °C ($p < 0.001$) and 20 °C ($p < 0.001$), and there was very little survival and no survival at 25 and 30 °C, respectively.

Similar to *S. mucronata*, *Moina* appears to use PER at all temperatures (Figure 2), with no statistical difference between the +PRR and the dark control at any temperature (Table 1). This suggests that *Moina*'s use of PER is not temperature-dependent. However, there was a statistically significant difference in survival in the −PRR across temperatures; specifically, survival was significantly higher at 10 °C compared to 15 °C ($p = 0.034$; Figure 2), and at 20, 25, and 30 °C, there was little to no survival in the −PRR (Figure 2). This indicates that dark repair and photoprotection in *Moina* are more effective at colder temperatures, similar to *S. mucronata*.

In contrast to *S. mucronata* and *Moina*, PER in *D. birgei* appeared to be low (Figure 3). At 15 °C, there was no difference in survival in the +PRR and −PRR, indicating no PER at this temperature (Figure 3(a); $F = 1.079$, $p = 0.339$). At the other temperatures, however, there was increased survival in the +PRR compared to −PRR (Table 1), indicating some use of PER. The use of dark repair and photoprotection appeared to be low at all temperatures, as indicated by little to no survival in

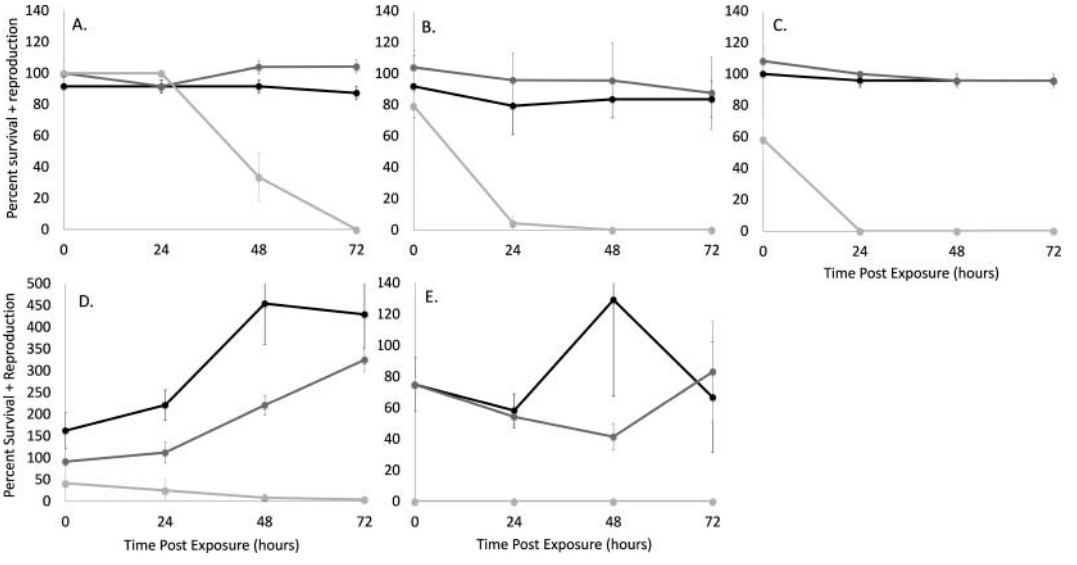

Figure 1. Mean percent survival and reproduction of *Scapholeberis mucronata* at five different temperatures: 10 °C (A), 15 °C (B), 20 °C (C), 25 °C (D; note the differing *Y*-axis scale), and 30 °C (E). Treatments were UV-B exposure followed by photorepair radiation (+PRR, dark grey line), UV-B exposure followed by dark conditions (−PRR, light grey line), or dark controls receiving no UV-B or PRR exposure (black line). *X*-axis is hours following the 24-hour PRR exposure period. Error bars indicate standard error ($n = 4$).

the −PRR (Figure 3). At all temperatures, dark repair and photoprotection were insufficient for the *D. birgei* in the −PRR to survive past 24 hours (Figure 3). During the UV-B and PRR exposure at 10 °C, none of the *D. birgei* in any of the treatments (+PRR, −PRR, and dark control) survived.

Discussion

We found that both *S. mucronata* and *Moina* appear to use PER effectively at a wide range of temperatures (10–30 °C), whereas *D. birgei* appears to have more limited use of PER and only at warmer temperatures (20–30 °C). Temperature is more important for UV-exposed *S. mucronata* and *Moina*

Table 1. Results of repeated measures analysis of variance (RM ANOVA; $n = 4$ for each experiment). Percent survival data (p) were log-transformed (log ($p + 1$)).

	Overall treatment effect		Time × treatment interaction	
Species and temperature	*F*	*P*	*F*	*p*
Scapholeberis				
10	38.097	0.000	19.811	0.000
15	98.901	0.000	25.047	0.000
20	2930.179	0.000	236.323	0.000
25	18.112	0.001	7.797	0.000
30	32.492	0.000	0.562	0.720
Moina				
10	5.375	0.029	5.929	0.005
15	428.391	0.000	61.669	0.000
20	113.140	0.000	0.591	0.648
25	9109.319	0.000	18.228	0.000
30	409.726	0.000	7.114	0.006
Diaphanosoma				
15	55.626	0.000	3.603	0.009
20	64.761	0.000	1.353	0.276
25	9.335	0.014	1.631	0.196
30	29.206	0.000	1.870	0.191

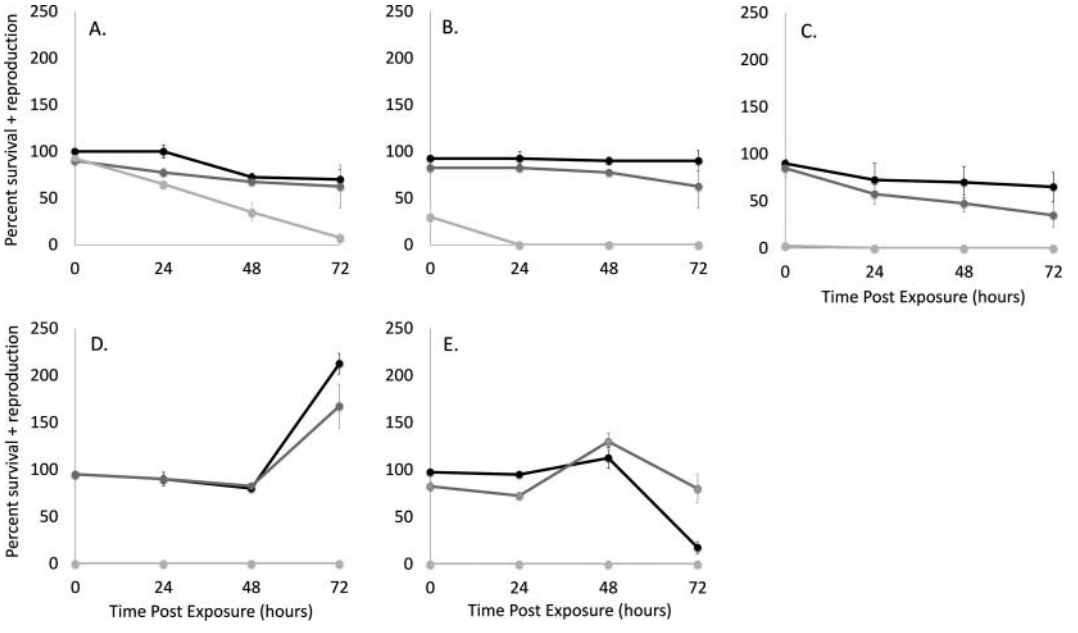

Figure 2. Mean percent survival and reproduction of *Moina* spp.at five different temperatures: 10 °C (A), 15 °C (B), 20 °C (C), 25 °C (D), and 30 °C (E). Treatments were UV-B exposure followed by photorepair radiation (+PRR, dark grey line), UV-B exposure followed by dark conditions (−PRR, light grey line), or dark controls receiving no UV-B or PRR exposure (black line). *X*-axis is hours following the 24-hour PRR exposure period. Error bars indicate standard error ($n = 4$).

in the −PRR, compared to the +PRR; specifically, our results indicate that dark repair and photoprotection may be more effective at colder temperatures for both taxa. *D. birgei*, on the other hand, exhibits almost no UV tolerance in the absence of PRR at any temperature. This result of *Diaphanosoma* being the most UV-sensitive genus is consistent with the findings from a Chilean lake, where *Diaphanosoma chilense* and *Moina micrura* were the most and least UV-sensitive, respectively, of four cladoceran taxa that were studied (Ramos-Jiliberto et al. 2004).

Contrary to our findings for *S. mucronata* and *Moina*, other studies have found that PER in *Daphnia* spp. is indeed temperature-dependent. For example, *D. pulicaria, D. middendorffiana, D. pulex*, and *D. parvula* exhibited higher rates of PER and survival at 10 °C compared to 20 °C after acute UV-B exposure (Connelly et al. 2009). On the other hand, MacFadyen et al. (2004) observed greater PER and reduced DNA damage at higher temperatures (25 vs. 15 °C and 5 °C) in *D. pulicaria*, which is consistent with our *Diaphanosoma* results. One possible explanation for these discrepancies could be that Connelly et al. (2009) administered a short (15-minute), high UV-B dose rate prior to PRR exposure, whereas MacFadyen et al. (2004) administered a longer (12-hour), lower UV-B dose rate concurrently with PRR exposure, which would allow DNA damage induction and repair to occur simultaneously. We followed Connelly et al.'s (2009) exposure conditions, which separate damage induction and repair into sequential steps.

Our result of the non-temperature dependence of PER in *S. mucronata* and *Moina* may differ from Connelly et al.'s (2009) results with *Daphnia* for several reasons. First, PER and the role of temperature vary across taxa. For example, similar to our results but in contrast to Connelly et al. (2009), PER did not vary with temperature in three macrophyte species exposed to UV-B (Van De Poll et al. 2002). Not only does UV response vary across taxa, but it can also vary across genotype within species. *Daphnia melanica* genotypes from high UV environments repaired UV-induced DNA damage faster that *D. melanica* from low UV environments due to more efficient PER of the former genotype (Miner et al. 2015). Second, the temperature acclimation procedures used in

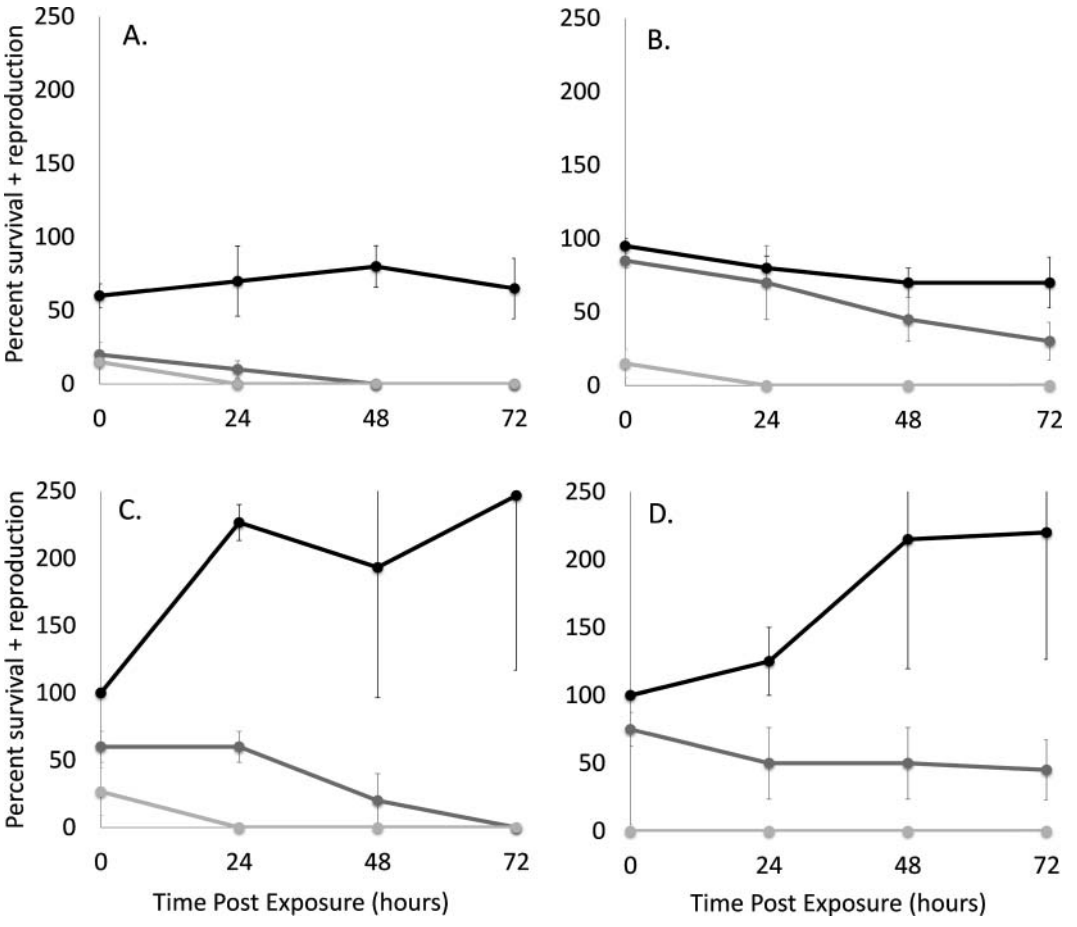

Figure 3. Mean percent survival and reproduction of *Diaphanosoma birgei* at four different temperatures: 15 °C (A), 20 °C (B), 25 °C (C), and 30 °C (D). Treatments were UV-B exposure followed by photorepair radiation (+PRR, dark grey line), UV-B exposure followed by dark conditions (−PRR, light grey line), or dark controls receiving no UV-B or PRR exposure (black line). *X*-axis is hours following the 24-hour PRR exposure period. Error bars indicate standard error ($n = 4$).

different studies, along with general thermal tolerances of each species, are likely important. Williamson et al. (2002) acclimated 1- or 2-day-old specimens to experimental temperatures for two days and MacFayden et al. (2004) acclimated adult *Daphnia* for three days, similar to our procedure. Connelly et al. (2009) cultured specimens of *Daphnia* for six months or more and acclimated them to the experimental temperatures from neonate to gravid stage to ensure if any temperature effects on the biological responses of the species were evident. They note that the temperature effects observed by MacFadyen et al. (2004) may have been restricted by a reduced acclimation time (Connelly et al. 2009). In our experiments, a reduced acclimation time may have been particularly important for *D. birgei*, which survived the 72-hour acclimation period at 10 °C but did not survive the 24-hour PRR exposure period (dark controls included). *D. birgei* abundance is positively correlated to temperature in some south-temperate systems (Davidson et al. 1998), and a closely related species, *Diaphanosoma brachyurum*, is known to be a stenothermic thermophile (Verbitskii et al. 2009).

Finally, in comparing our results to other studies, it is important to note the differences in experimental UV-B and PRR exposure conditions. Although our UV-B dose and the sequential, rather than concurrent, timing of UV-B and PRR exposures were similar to other studies (e.g. Huebner et al. 2006; Connelly et al. 2009), one issue with our study is the inconsistent PRR dose used across

experiments as a result of our malfunctioning 365 nm UV-A lamp. Most other PER studies have used a combination of UV-A and visible radiation for their PRR treatments (MacFadyen et al. 2004; Huebner et al. 2006; Connelly et al. 2009), although Ramos-Jiliberto et al. (2004) used only the visible portion of a solar simulator lamp to induce PER. The photolyase enzyme involved in PER has chromophores with peak absorption at 380 and 440 nm, and thus photoreactivation occurs via blue-light absorption (Sinha and Häder 2002). We did not have access to a scanning spectral radiometer, but it is likely that most of the effective PRR dose came from the six cool white lamps in our experiment. *Moina* spp. received PRR only from these lamps and exhibited equivalent survival in the +PRR and dark controls at all temperatures. *S. mucronata* received PRR that included UV-A at 15, 25, and 30 °C and PRR without UV-A at 10 and 20 °C and the survival data suggest that PER occurred equally well at all temperatures regardless of the UV-A lamp. Nevertheless, comparisons of our trials across species and temperature should be done cautiously, as other work has shown that PRR duration affects survival (Huebner et al. 2006), meaning that PRR dose is important.

Survival of *S. mucronata* and *Moina* spp. in the −PRR was significantly higher at 10 °C than at warmer temperatures. This indicates that both *S. mucronata* and *Moina* spp. are better able to utilize dark repair and/or photoprotection strategies at lower temperatures and is consistent with Connelly et al.'s (2009) finding that *D. pulicaria* only exhibited slight dark repair at 10 °C and none at 20 °C. Connelly et al. (2009) point out that a high initial UV-B dose can overwhelm the molecular machinery of NER. We were unable to quantify the acute UV-B dose used in our experiment, but it is likely similar to 9.3 kJ m^{-2}, the highest dose used by Connelly et al. (2009). We used the same UV-B lamp model, exposure time, and lamp location (24 cm above the organisms), although we only used one lamp with no screens, whereas Connelly et al. (2009) used three lamps with wire-mesh screens. *D. birgei* seemed to be the most sensitive taxon to this high UV-B dose, exhibiting little evidence of dark repair and/or photoprotection; in fact, it did not survive past 24 hours in the −PRR at any temperature. This is consistent with the results of Ramos-Jiliberto et al. (2004), which showed that *D. chilense* was the most UV-sensitive species in the absence of PRR.

For all three species, we selected the largest, non-egg-bearing individuals of similar body size for each experiment. It is possible, however, that there may have been some inconsistencies in the life stages used. This is important because individuals at varying life stages may have different PER efficiencies. Studies have shown that in some zooplankton species, juveniles have significantly less effective use of PER mechanisms compared to adults, which exhibited higher survival rates after UV-B exposure compared to juveniles (Grad et al. 2003; Ramos-Jiliberto et al. 2004). Both of these studies took the largest individuals of the populations to represent adult life stages as we did in our experiment. If some juvenile individuals were inadvertently selected for a treatment, this could lead to higher mortality rates in treatments that had more juveniles in the group. It could also lead to differing reproduction rates over the course of the experiment. It is notable that at 25 and 30 °C, there was substantial *D. birgei* reproduction in the dark controls, but little to none in the UV-exposed treatments, even in the +PRR. This suggests that UV exposure not only affects survival, but also reproduction of *D. birgei*. Such UV effects on reproduction have also been observed in *Daphnia* (Huebner et al. 2009; Huebner et al. 2013).

The ability to perform PER equally well at a broad range of temperatures, instead of just at cooler temperatures, may be particularly beneficial for littoral, surface-dwelling *S. mucronata*. Unlike many pelagic zooplankton species, *Scapholeberis* spp. are not known to undergo diel vertical migration (DVM) below the thermocline; instead, they remain in the warmer, potentially high-UV surface waters as part of the neuston community throughout the seasons (Von Ende 2001). Similarly, broad PER capabilities would benefit *Moina* spp., which may or may not undergo DVM (Kelso et al. 2003; Semyalo et al. 2009), and thus may be found across a range of temperatures, PRR levels, and UV-B levels. The more limited PER capabilities of *Diaphanosoma* spp. may be compensated for by DVM in clear, high-UV systems (Boeing et al. 2004).

Climate change continues to play an increasingly critical role in the aquatic environment. These results provide a better understanding of how these freshwater cladocerans may respond to

temperature and UV changes in their habitats due to climate change. We have observed how temperature may play a role in PER and dark repair effectiveness, but that is only one variable that can influence UV responses of these organisms. It is important that future work examines other variables, such as genotype and life stage, that can potentially influence the effectiveness of PER and other mechanisms that these organisms use to cope with the stresses of UV-B radiation.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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