

Shedding light on environmentally transmitted parasites: lighter conditions within lakes restrict epidemic size

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Abstract. Parasite fitness depends on a successful journey from one host to another. For parasites that are transmitted environmentally, abiotic conditions might modulate the success of this journey. Here we evaluate how light, a key abiotic factor, influences spatiotemporal patterns of zooplankton disease where light varies seasonally, across lakes, and with depth in a lake. In an *in situ* experiment using those three sources of variation, we tested sensitivity of spores of two parasites to ambient light. Infectivity of both parasites was lower when exposed to ambient light in comparison to parasites exposed to otherwise similar conditions in the dark. The more sensitive parasite (the fungus, *Metschnikowia*) was damaged even under lower ambient light during late fall (November). With this differential sensitivity established, we evaluated links between light environment and natural outbreaks in lakes. Consistent with the incubations, epidemics of the less sensitive parasite (the bacterium, *Pasteuria*) started earlier in the fall (under higher ambient light), and both parasites had smaller outbreaks in more transparent lakes. Overall, light environment may impact the timing and size of disease outbreaks. Outbreaks could thus become exacerbated by human activities that darken waters, including lake browning associated with climate change and eutrophication.

Key words: climate change; *Daphnia*; dissolved organic matter; lakes; light; parasite.

INTRODUCTION

Free-living stages of parasites often must survive wide-ranging environmental conditions in nature while awaiting encounters with new hosts. Because outside-of-host environments often vary more extremely than within-host conditions, this free-living stage can pose challenges for parasites. Transmission stages of some parasites can be well protected from environmental conditions (e.g., helminths: Pietrock and Marcogliese 2003; *Cryptosporidium*: King and Monis 2007). However, for many parasites with environmental stages, abiotic factors can harm their fitness, for example, low temperatures (lungworm: Kutz et al. 2002), high humidity (influenza: Lowen et al. 2007), and low salinity (cholera: Miller, Drasar, Feachem, 1982). If changing climatic conditions alter these abiotic constraints on parasite fitness, climate change could alter the timing and magnitude of disease epidemics (Williamson et al. 2017).

Light can pose a key environmental constraint on the survival of free-living stages of parasites (Ruelas et al. 2007, van Dijk et al. 2009, Overholt et al. 2012, Studer et al. 2012, Williamson et al. 2017). Light intensity varies spatially and temporally, with dramatic consequences for populations, communities, and ecosystems (Häder et al. 2007, 2015, Williamson et al. 2019). Light can damage organisms, as certain wavelengths become lethal at high doses. Indeed, humans use ultraviolet (UV) radiation to kill pathogenic organisms (Yaun et al. 2004). Hence, light may mediate interactions between hosts and environmentally transmitted parasites (Häder et al. 2015, Williamson et al. 2017). Hosts and parasites may differentially resist or avoid light damage (e.g., through protective molecules: Karentz et al. 1991, Zellmer 1995, Jacobs et al. 2007; or migration: Bebout and Garcia-Pichel 1995, Storz and Paul 1998). They also can differ in their ability to repair damage (Roy 2000). Thus, changing light conditions may impact the interactions between hosts and parasites either by impacting the infectivity of parasites or the susceptibility of hosts (Bruning 1991, Tucker and Williamson 2011, Debecker et al. 2015).

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Several ecosystem features affect the light environment. Exposure to potentially harmful wavelengths of sunlight in natural ecosystems is largely controlled by sun angle (latitude, time of day, time of year) and cloud cover. In aquatic environments, those features govern incident light to the water surface. Exposure to light in the water column then becomes depth-dependent, as absorption means that deeper waters experience less light. Notably, light is absorbed and scattered by dissolved and particulate compounds (including algae). Some of these compounds, especially dissolved organic matter (DOM), selectively absorb UV radiation (Kirk 1993). DOM therefore protects organisms within lakes from these potentially more harmful shorter wavelengths. The concentrations of compounds like DOM, phytoplankton, etc., vary both through time (Kalf and Knoechel 1978, Sommer 1985, Couture et al. 2012) and across a landscape (Morris et al. 1995, Dodson et al. 2000, Laurion et al. 2000, Xenopoulos et al. 2003). Notably, many lakes are becoming darker because of human activities (Monteith et al. 2007, Larsen et al. 2011, Strock et al. 2014, 2016, Solomon et al. 2015, Schindler et al. 2016, Weyhenmeyer et al. 2016, Kritzberg 2017).

Changes to the light environment may alter disease dynamics in lakes by removing light as a constraint on environmentally transmitted parasites (Williamson et al. 2017). To evaluate this potential, we examined light effects on fitness of free-living stages of parasites and natural outbreaks along light gradients. In the focal system, *Daphnia* hosts migrate deep into the water column during the day (Lampert 1989, Williamson et al. 2011), greatly reducing their UV exposure (Storz and Paul 1998, Rhode et al. 2001, Leech et al. 2005). However, the infective propagules (hereafter: spores) of the two focal parasites, *Pasteuria ramosa* and *Metschnikowia bicuspidata* (hereafter: *Pasteuria* and *Metschnikowia*) cannot swim. Thus, they cannot behaviorally escape light exposure. Although both parasites can reach epidemic prevalence in *Daphnia* populations in autumn (Cáceres et al. 2006, Auld et al. 2014), both are sensitive to UV and photosynthetically active radiation (PAR; Overholt et al. 2012, 2020). Though *Daphnia* survival can be reduced by high levels of UV radiation when exposed (Williamson et al. 2001, Overholt et al. 2012), low levels of UV radiation do not impact host susceptibility to *Metschnikowia*, and *Metschnikowia* is much more sensitive to radiation than is *Daphnia* (Overholt et al. 2012). The present study extends prior work (Overholt et al. 2012, 2020), which focused on a single parasite at a time. In this study, we ask whether light shapes the relative dynamics in multiparasite systems. To evaluate relative sensitivity of these parasites to light over the epidemic season, we experimentally incubated parasite spores in lakes in July, August, and November (i.e., decreasing incident light across the epidemic season) in light-exposed vials (or covered vials as a control) and then used them to infect hosts in the lab, quantifying spore

infectivity. Then, with field survey data, we examined the relationship between lake transparency and parasite dynamics. We expected that epidemics would start later (i.e., as the light constraint waned autumnally) and remain smaller in more transparent lakes.

METHODS

Hosts and parasites

The host, *Daphnia dentifera*, is common in Midwestern (United States) lakes. It is susceptible to parasites including *Pasteuria ramosa* (a bacterium) and *Metschnikowia bicuspidata* (a fungus). Both parasites share similar infection mechanisms and life cycles. For instance, both infect their hosts by penetrating the digestive tract after being accidentally consumed during host feeding (Metschnikoff 1884, Duneau et al. 2011). Then, both replicate in the hemolymph of hosts, filling host bodies with spores (Ebert 2005). Most important for this study, upon host death those spores are released into the water column where they can be consumed by a new host, completing the infection cycle (Metschnikoff 1884, Ebert 2005). In laboratory conditions, spores of both parasites are long-lived relative to the length of an epidemic (Duffy and Hunsberger 2019), but in stratified lakes, they may sink out of the water column to lake sediments unless conditions are turbulent. It is while the parasite is in the water column during environmental dispersal that light could most strongly impinge on epidemics via direct effects on spores.

Lake transparency measurements and metrics

In order to quantify light exposure for parasites in the incubation experiment, we measured within-lake light attenuation and surface-level ambient light during incubations. Within-lake attenuation of both UV (320 nm) and PAR (400–700 nm) was measured directly (submersible radiometer model BIC 2104, Biospherical Instruments, San Diego, CA, USA; Appendix S1: Section S1). Each metric was converted to a percent of incident light remaining at incubation depth (0.5 and 2 m). Surface-level incident 320 nm UV and PAR was integrated over 3-min time intervals by a radiometer (Model 2104RL; Biospherical Instruments, San Diego, CA, USA) deployed at the Greene Sullivan State Forest ranger station located within 10 miles of all experimental lakes (Appendix S1: Section S1, Table S1). Cumulative surface-level incident UV and PAR are documented for each incubation in Fig. 1 and in Appendix S1: Table S1. We multiplied percent incident light at incubation depth and surface-level incident light measurements to obtain within-lake light exposure for 320 nm UV and PAR separately (Appendix S1: Section S3).

For the field survey we indexed lake transparency as the depth at which 1% of incident 320 nm UV remained. To calculate this index, we measured the absorbance of

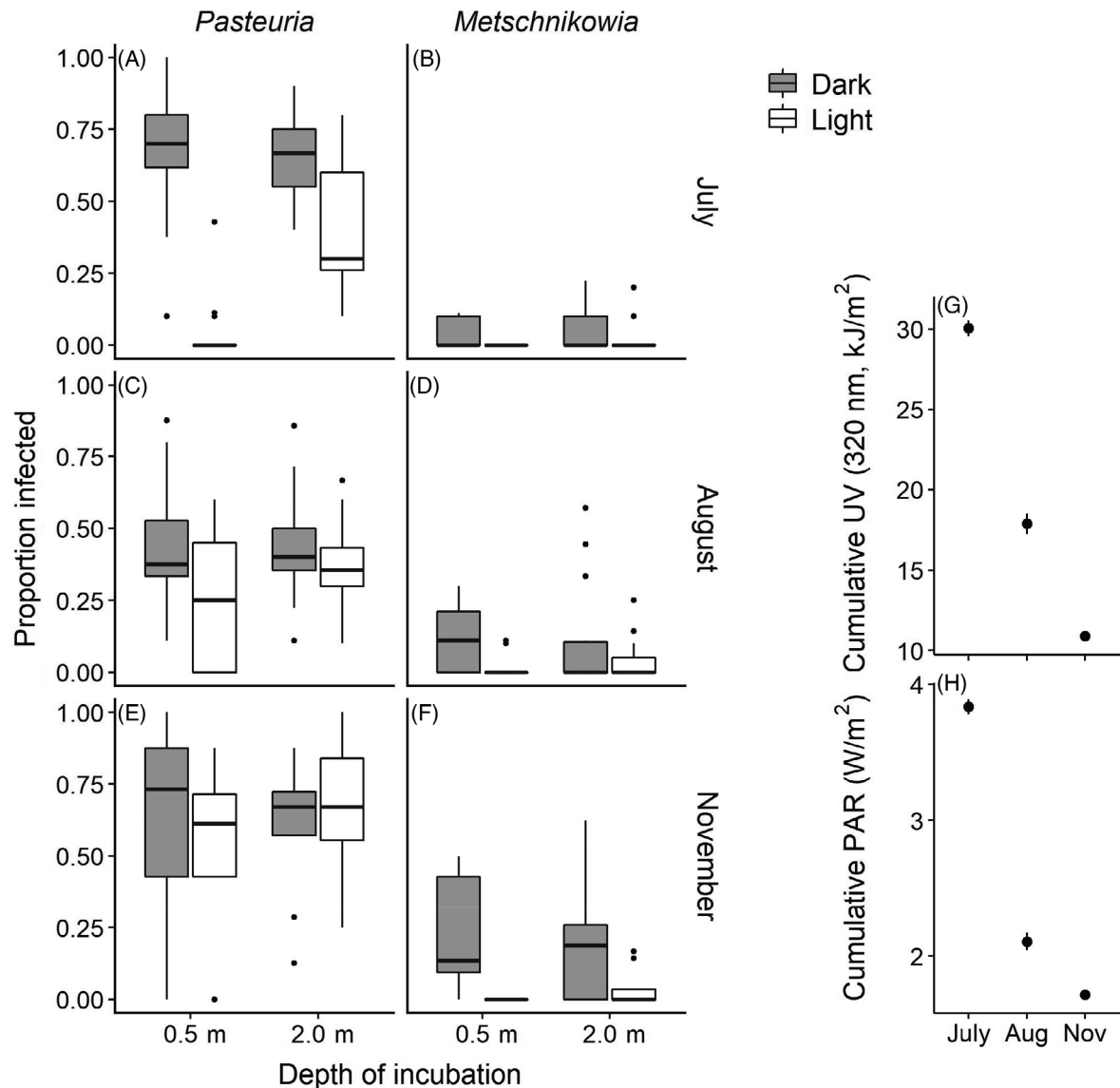


FIG. 1. Light exposure decreased the proportion of *Daphnia* hosts infected by spores of both parasites. For the bacterium *Pasteuria* (A, C, and E), light exposure decreased the proportion of hosts infected in (A) July and in (C) August, but not in (E) November. Additionally, for light-exposed vials (white bars), fewer animals became infected from spores incubated at lighter 0.5 than at darker 2m depth in (A) July only. For the fungus *Metschnikowia* (B, D, and F), light-exposed spores infected fewer animals than spores in the dark treatment (gray bars) in all months (July, August, and November; no additional depth effects were found). Data from vials incubated in all lakes are pooled by light treatment in box plots. (G and H) Cumulative ambient 320 nm UV and PAR ($\times 10^7$) in each incubation decreased as autumn progressed. Error bars (SD) correspond to cumulative differences in surface-level UV and PAR along lakes.

320nm UV light of filtered lake water samples (using filtrate from lake epilimnia (Whatman glass microfiber filters, Grade GF/F) and a Shimadzu UV/ Visible UV-1650 PC spectrophotometer). With these absorbance values, we estimated light penetration in the water column (with Beer-Lambert law; Appendix S1: Section S1). More transparent (lighter) lakes have deeper values for 1% 320 nm UV remaining (largerscaled transparency

values). Attenuation of 320 nm UV and of PAR are correlated in our study lakes ($r^2 = 0.80$, $P < 0.001$). Thus, darker lakes have both less UV and less PAR. To characterize incident light, we calculated daily maximum short-wave radiation from the AmeriFlux site at Morgan Monroe State Forest, Indiana (60 miles from study lakes; Roman et al. 2015). These data provide a visual descriptor of light throughout autumn and among years.

Spore incubation methods

We incubated spore slurries of each parasite in lakes to assess their infectivity after exposure to ambient sunlight in situ in July (20–25), August (15–20), and November (31 October–5 November 2016). We selected five lakes along a gradient of water transparency: Airline, Canvasback, Beaver Dam, Goodman, and Midland lakes (Appendix S1: Section S1, Table S1). Six quartz vials filled with *Pasteuria* or *Metschnikowia* spore slurries were suspended at 0.5 and 2m depths in each lake, for a total of 24 vials per lake (6 per parasite per depth). Half of these vials were covered in dark plastic (dark treatment); the others were left uncovered, and hence exposed to ambient light at depth (i.e., PAR + UV; light treatment; see Appendix S1: Section S2 for additional details). Parasite spore slurries were composed of infected lab animals that were ground in lake water to release spores. These slurries were pipetted into vials such that each *Pasteuria* vial contained 300,000 spores in each incubation month and each *Metschnikowia* vial contained 15,000 spores in the July incubation and 37,500 spores in August and November incubations.

After the incubation period, incubated spore slurries as well as algal food (*Ankistrodesmus falcatus*) were added to 150 mL filtered lake water, yielding spore concentrations of 2000 spores/mL of *Pasteuria* and 100 spores/mL of *Metschnikowia* in July and 250 spores/mL of *Metschnikowia* in August and November. *Metschnikowia* spore dose was increased in August and November because of low infection levels in the control treatment in July, with both 100 and 250 spores/mL being within the range typically used in lab experiments (Shocket et al. 2018, Duffy and Hunsberger 2019). This water-algae-spore mixture was distributed among either 10 (July and August incubations) or 8 (November) 15mL centrifuge tubes. For both parasites, we placed 3–4-day-old, individual *Daphnia* of a clone ('Mid37') that is susceptible to both parasites into the tubes. After 24 h of exposure at 20°C, we moved *Daphnia* to 50mL tubes. We maintained each individually (still at 20°C) with daily feeding and water changes every other day until visual diagnosis of infection (Appendix S1: Section S2).

We used generalized linear mixed models (GLMMs) with binomial error structures to test the effects of light treatment (light-exposed or covered vials), depth, and month on host infection status. The first model evaluated which parasite was more sensitive to light. Hence, only parasite, light treatment, and the interaction were included as fixed effects with a lake by month interaction as a random effect. Then, we evaluated each parasite separately. The second set of models fit light treatment, depth, month, and their interactions as fixed effects for each parasite (retaining the lake by month interaction as a random effect). Finally, in a third set of models, data were analyzed for each month separately with otherwise similar fixed and random effects. All significant interaction terms were included that still allowed for model

convergence. Note that for these analyses, lake-specific light conditions were not included. An additional analysis evaluated the effects of light exposure in lakes on relative infectivity of light-exposed spores as compared with those in covered vials (Appendix S1: Section S3). All statistics were performed in R Version 3.5.3 (R Core Team, 2019). GLMMs were performed with the lme4 package (Bates et al. 2015).

Field survey

We used a field survey to link light sensitivity of parasites to the timing and size of parasite outbreaks in lakes. We sampled 37 lakes in south central Indiana (Greene and Sullivan counties) approximately every 2 weeks, August–November, during 2014–2016 (Appendix S1: Section S4); these lakes all stratify during summer, but stratification breaks down in early fall in some of the shallower lakes. Notably, this is substantially more lakes and years than in a related earlier study: the Overholt et al. (2012) study focused on 18 lakes in a single year. At each sample date, we pooled three vertical plankton tows (each from the bottom of the lake up through the surface); each of the tows was collected at least 25 m apart with a Wisconsin net (13 cm diameter, 153 micron mesh). From those tows, we visually diagnosed live *D. dentifera* from subsamples of the entire collection for late-stage infection using a dissecting microscope (40–50X). We define “outbreak size” as the maximum prevalence of infection during the season. Epidemics (“large” outbreaks) “started” on the first date at which infection prevalence reached and remained above 1% for at least one more visit (Duffy et al. 2005). “Small” outbreaks did not maintain prevalence above 1% for more than one visit.

We compared start dates of epidemics between parasites with a linear mixed effects model. In this model, epidemic start date was the response variable, parasite identity was a fixed effect, and year and lake were random effects (nlme package in R; Pinheiro et al. 2018). A paired *t* test was also used to compare start dates of parasites in lake-years where epidemics of both parasites occurred. This smaller subset of lakes controls for within-lake factors that could also influence epidemic start dates. For each parasite, we also fit binomial generalized linear mixed effects models to link our index of lake transparency (depth of 1% 320 nm UV remaining) to maximum infection prevalence (lme4 package; Bates et al. 2015). In global models, maximum prevalence was predicted by transparency, epidemic start date, lake depth, mean host density, mean chlorophyll concentrations, and year as fixed effects and an observation level random effect to mitigate overdispersion (Harrison et al. 2018). All fixed effects except year were centered and scaled. Results from the model with the lowest AIC are presented in the text with predicted effects of fixed effects displayed with the jtools package in R (Long 2019). Effects of the predictors were found to be

qualitatively similar to their effects in the global model and various subsets of it (Appendix S1: Section S5). To evaluate whether high transparency inhibited epidemics (“large” outbreaks; see above), we used a t test to compare the transparency of lakes with epidemics to lakes with small or nonexistent outbreaks.

RESULTS

Spore incubations

Spores of both parasites were less infective after incubation in ambient light, but the infectivity of *Metschnikowia* was reduced more. This differential sensitivity to light appeared as a significant interaction between parasite and light treatment (parasite $\times$ light: $z = 2.71$, $P = 0.007$). Additionally, infectivity of *Metschnikowia* was still reduced by incident light in late summer (August) and fall (November; Fig. 1D, F). In contrast, the impact of incident light on *Pasteuria* decreased as the season progressed (Fig. 1, left panels). More specifically, compared to July incubations, light-exposed *Pasteuria* spores infected a greater proportion of hosts in August ($z = 5.42$, $P < 0.001$; compare Fig. 1A,C) and November ($z = 6.76$, $P < 0.001$; compare Fig. 1A,E). The diminishing seasonal impact of light on *Pasteuria* also manifested in the separate analyses of months. In July, spores exposed to ambient light were less infective (light: $z = -8.26$, $P < 0.001$), especially at shallower depths where light was greater (light $\times$ depth: $z = 5.61$, $P < 0.001$; Fig. 1A). Though incident light declined in August (Fig. 1G), the main effect of light remained ($z = -3.41$, $P < 0.001$; Fig. 1C). However, in still darker November, light no longer constrained success of *Pasteuria* (light: $z = -1.00$, $P = 0.318$; light $\times$ depth: $z = 1.13$, $P = 0.259$; Fig. 1E). Thus, exposure to ambient light reduced infectivity of *Pasteuria* spores in summer, but by late autumn, this inhibitory effect on *Pasteuria* disappeared.

The fungal parasite *Metschnikowia* was more sensitive to light. Light damaged spores throughout the epidemic season (light: $z = -4.42$, $P < 0.001$), but depth provided some protection from light damage (light $\times$ depth: $z = 2.50$, $P = 0.013$). Both August ($z = 1.96$, $P = 0.050$; Fig. 1D) and November ($z = 3.27$, $P = 0.001$; Fig. 1F) showed higher overall proportion of infected hosts compared to July when the spore dose was lower (Fig. 1B; see Methods). However, light remained a strong constraint throughout autumn: even in later, darker months, spores from light-exposed treatments were less infective than spores from covered treatments (Fig. 1B, F). In each month analyzed separately, spores exposed to light infected a smaller proportion of hosts in July ($z = -1.99$, $P = 0.047$; Fig. 1B), August ($z = -3.67$, $P < 0.001$; Fig. 1D), and November ($z = -4.00$, $P < 0.001$; Fig. 1F); no depth or depth $\times$ light interactions were significant likely because we did not have the statistical power to detect these effects with the data subsetted by

month. Overall, unlike for *Pasteuria*, light continued to significantly impact the infectivity of *Metschnikowia* spores well into autumn.

Field survey

We predicted that differential light sensitivity of parasites would impact timing of outbreaks. Specifically, because incident light levels wane in late summer and autumn, epidemics should start earlier for the less sensitive *Pasteuria* than for the more sensitive *Metschnikowia*. Indeed, the median start date for *Pasteuria* epidemics was 16 days earlier than for *Metschnikowia* in 2014 (22 September compared to 6 September), 16 days in 2015 (11 September compared to 26 August), and 24 days in 2016 (10 October compared to 16 September; Fig. 2). Thus, epidemic start date differed significantly between parasites ($t = 3.84$, $df = 8$, $P = 0.005$; Fig. 2B). In lakes with epidemics of both parasites in the same year, those of *Pasteuria* started on average 23 days earlier ($t = 4.3$, $df = 8$, $P = 0.003$; Fig. 2C).

Because both parasites were sensitive to light, we tested two hypotheses. First, we expected epidemics (larger outbreaks) of a given parasite to start later in lighter lakes (i.e., more transparent, with deeper light penetration). In these lakes, higher light levels should more effectively kill spores for a longer portion of the year. Second, outbreaks should remain smaller in lighter lakes, because of direct mortality effects on spores. For *Pasteuria*, too few outbreaks qualified as epidemics to test for the effect of start date on epidemic size. However, less transparent lakes had larger outbreaks (Likelihood-ratio Test (LRT) = 30.95, $P < 0.001$; Fig. 3A). Furthermore, lakes with *Pasteuria* epidemics were less transparent than those with just minor outbreaks ($t = -4.92$, $P < 0.001$; Fig. 3A). Small outbreaks in general may have made it more difficult to detect effects of the other covariates that were originally included in the global model (Appendix S1: Section S5).

For *Metschnikowia*, though epidemics did not start earlier in darker lakes ($F = 0.95$, $P = 0.34$), darker lakes had larger epidemics (LRT = 6.52, $P = 0.011$, Fig. 3B). Epidemic size was also associated with epidemic start date (earlier starting epidemics grew larger: LRT = 11.36, $P < 0.001$, Fig. 3C), lake depth (deeper lakes had larger epidemics: LRT = 7.91, $P = 0.005$, Fig. 3D), and host density (lakes with higher host densities had larger epidemics: LRT = 8.78, $P = 0.003$, Fig. 3E).

DISCUSSION

Light impacts many environmentally transmitted parasites. In some cases, light damages free-living stages. In these cases, waters darkened by human activities could unleash larger disease outbreaks. To understand this possibility better, we evaluated light effects on parasite outbreaks in Midwestern lakes with an incubation

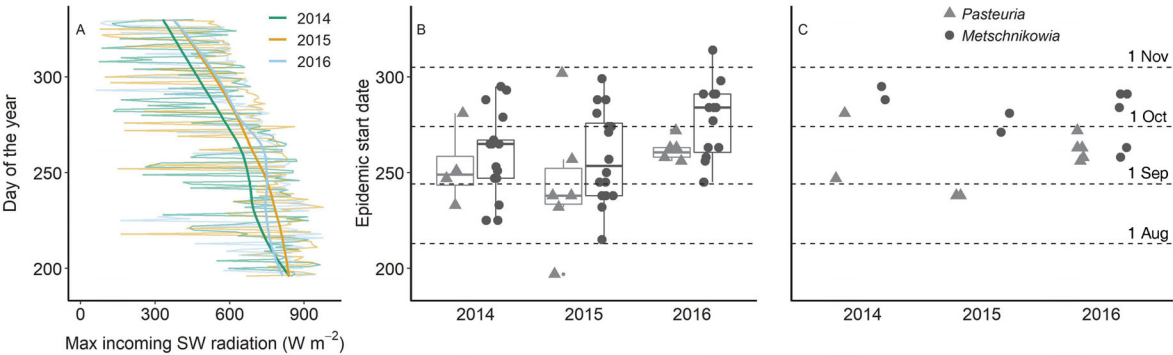


FIG. 2. Epidemics of the less light-sensitive bacterium *Pasteuria* started earlier than those of the more sensitive fungus, *Metschnikowia*. (A) Maximum short-wave (SW) radiation decreases autumnally near the study lakes (Morgan Monroe State Forest, Indiana; Roman et al. 2015). Loess trendlines accompany data from each year of the survey (2014, 2015, and 2016). Epidemics of *Pasteuria* started earlier in (B) lakes that showed epidemics of either parasite and in (C) lakes with epidemics of both in the same year. Dashed lines denote the first day of August (lowest), September, October, and November (highest day, as labeled).

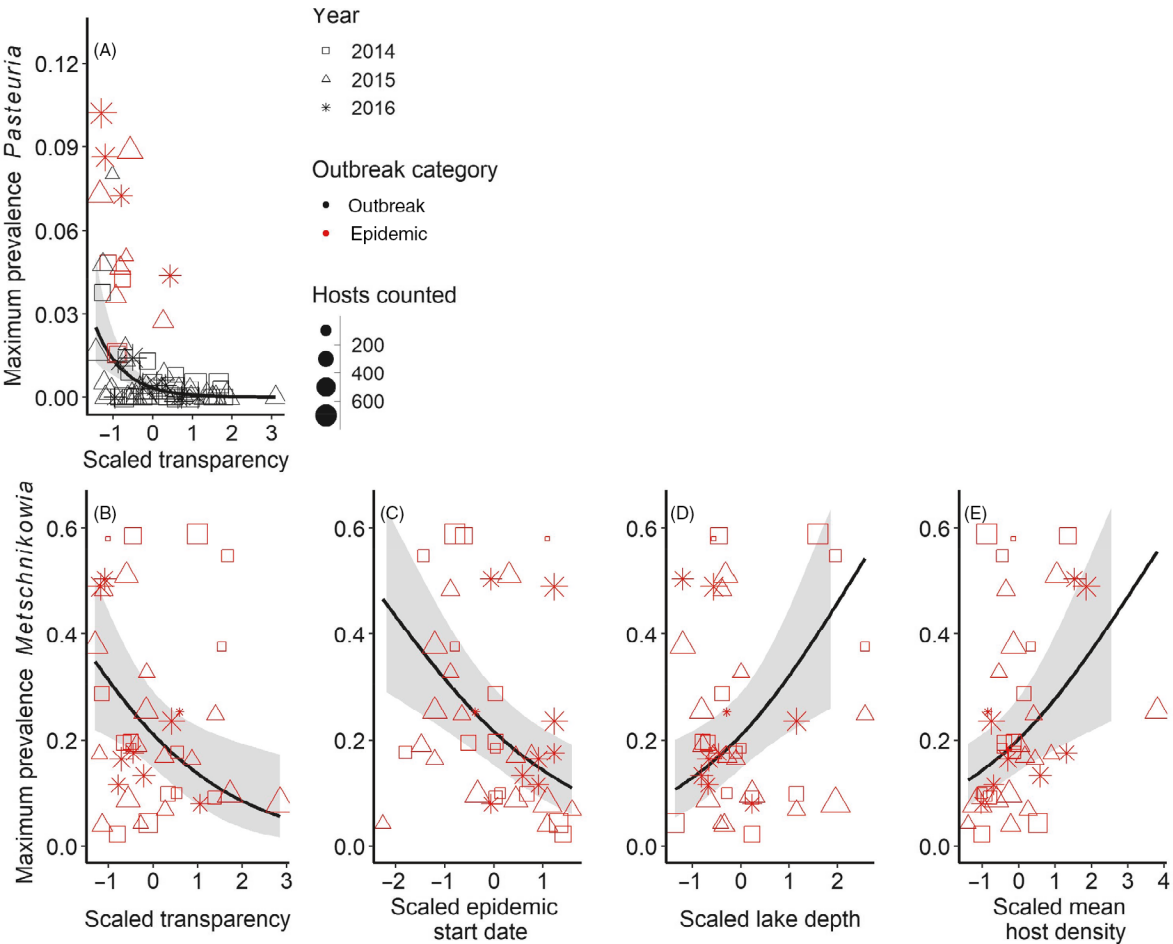


FIG. 3. Outbreaks (small = black; epidemics = red) in lakes in 2014–2016 became larger in darker lakes (i.e., those with lower-scaled indexes of lake transparency). (A) *Pasteuria* and (B) *Metschnikowia* epidemics became larger in less-transparent lakes. (C) *Metschnikowia* epidemics were also larger when they started earlier, (D) when in deeper lakes, and (E) in lakes with higher host densities. Trendlines with 95% confidence intervals reflect predicted effects of fixed effects.

experiment and a field study. Both parasites responded sensitively to ambient light conditions in summer (July). For the more sensitive *Metschnikowia*, these effects persisted even into November. Consistent with this differential sensitivity, we found that *Pasteuria* epidemics began earlier in the fall (when light levels begin to decrease). Furthermore, transparent lakes had smaller outbreaks of both parasites.

In the incubation experiment, light reduced the infectivity of parasite spores (especially *Metschnikowia*). We did not separate UV from PAR effects here, but both likely reduced spore infectivity. UV is typically more damaging, interfering with replication and transcription of DNA (Sinha and Häder 2002). However, despite only shallow penetration of UV (see Appendix S1: Fig. S2), spores still suffered reduced infectivity when incubated at 2m depth, and *Metschnikowia* experienced reduced infectivity even in late autumn (when incident UV was negligible). Thus, PAR likely damaged spores too, which is consistent with evidence from laboratory experiments on *Metschnikowia* and *Pasteuria* (Overholt et al. 2012, 2020). Differential sensitivity among parasites may stem from differences in protective or repair mechanisms. For instance, *Pasteuria* resides in the *Bacillus* clade (Ebert et al. 1996), where species resist UV through several mechanisms (Nicholson et al. 2000, Setlow and Li 2015). Some fungi tolerate UV well (Onofri et al. 2007) because of protective pigments, etc. (Ruisi et al. 2007). However, other *Metschnikowia* species do not produce high levels of these compounds, even in high-UV Antarctic conditions (Villarreal et al. 2016). It is also possible that incubated spores were exposed to additional differing conditions in clear and covered vials. Uncovered vials might have remained more oxygenated (because of algal photosynthesis), but *Pasteuria* spores are viable from deoxygenated sediments (Decaestecker et al. 2004), so this possibility is unlikely to have impacted *Pasteuria* spore infectivity. Though similar evidence has not been documented for *Metschnikowia*, spores of this parasite remain viable without reduced infectivity when stored in tubes in the refrigerator for many weeks (Duffy and Hunsberger 2019). Uncovered vials may also have had more reactive oxygen species generation due to reactions involving light and dissolved organic matter within the vials. Reactive oxygen species have been found to be effective for deactivation of some viruses (Kohn et al. 2016); this could be an additional mechanism at work in this system and warrants further study. However, other studies exposing our parasites to light in the laboratory setting indicate that light rather than reactive oxygen species is a key mechanism for reducing infectivity (Overholt et al. 2012, 2020).

Our study focused on the impacts of ambient light on parasite spores, but disease outcomes will depend on interactions between both hosts and parasites. Importantly, in this system, *Daphnia* migrate to deep waters during the day, reducing their UV exposure (Lampert 1989, Rhode et al. 2001). *Daphnia* also do not experience

altered susceptibility to *Metschnikowia* after exposure to low levels of UV (Overholt et al. 2012). However, changing light conditions may indirectly affect disease in *Daphnia* through a variety of mechanisms (Tucker and Williamson 2011). For instance, the production of reactive oxygen species through a reaction of light with dissolved organic compounds can induce a stress response in *Daphnia magna* (Saebelfeld et al. 2017), which might impact susceptibility to parasites (Lafferty and Holt 2003). Changes in algal food quality in response to light (Durif et al. 2015) might also affect host susceptibility or within host growth (Sánchez et al. 2019). However, even if other mechanisms are also at play, the combination of prior lab experiments (Overholt et al. 2012, 2020), our field experiments, and our lake survey all consistently point to light reducing parasite infectivity, with an overall outcome of reduced disease in clearer lakes.

The sensitivity of *Metschnikowia* and *Pasteuria* to damage by light is not unusual. Indeed, many pathogens of humans have water-borne stages that are vulnerable to light damage (e.g., *Schistosoma mansoni*, Ruelas et al. 2007; *Cryptosporidium parvum*, King et al. 2008; *Vibrio cholerae*, Berney et al. 2006). By reducing light damage to pathogens, browning waters may unleash epidemics of aquatic parasites infecting wildlife and humans (Williamson et al. 2017). Light also affects disease in terrestrial systems. For example, transmission of a virus of forest tent caterpillars was reduced in lighter environments (e.g., near edges and in patchy fragments) relative to darker interiors of forests (Roland and Kaupp 1995). Corsican pine also showed higher rates of a fungal disease on north facing (darker) slopes, and in an artificial shading experiment (Read 1968). Furthermore, light might be shaping patterns of disease even within individuals, since most fungal diseases occur on protected parts of plants, like the undersides of leaves (Manning and Tiedemann 1995). Hence, habitat-driven light environment may shape disease in both aquatic and terrestrial systems.

In this study, light reduced infectivity of spores of two parasites, and higher lake transparency was associated with reduced epidemic size for both parasites. Global climate change is making lakes darker; these less transparent lakes could become sicker lakes. Epidemics in *Daphnia* can exert ecosystem-level effects (Duffy 2007), so larger epidemics could impact food webs and lake ecosystems. More broadly, human activity continues to alter light penetration into numerous systems (e.g., smog near cities, deforestation, browning of surface waters, eutrophication, light pollution). These human-caused changes in light might affect disease by altering the survival of environmentally transmitted parasites.

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LITERATURE CITED

- Auld, S. K. J. R., S. R. Hall, J. Housley Ochs, M. Sebastian, and M. A. Duffy. 2014. Predators and patterns of within-host growth can mediate both among-host competition and evolution of transmission potential of parasites. *American Naturalist* 184:S77–S90.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bebout, B. M., and F. Garcia-Pichel. 1995. UV B-induced vertical migrations of cyanobacteria in a microbial mat. *Applied and Environmental Microbiology* 61:4215–4222.
- Berney, M., H. U. Weilenmann, A. Simonetti, and T. Egli. 2006. Efficacy of solar disinfection of *Escherichia coli*, *Shigella flexneri*, *Salmonella Typhimurium* and *Vibrio cholerae*. *Journal of Applied Microbiology* 101:828–836.
- Bruning, K. 1991. Infection of the diatom *Asterionella* by a chytrid. I. Effects of light on reproduction and infectivity of the parasite. *Journal of Plankton Research* 13:103–117.
- Cáceres, C. E., S. R. Hall, M. A. Duffy, A. J. Tessier, C. Helmle, and S. MacIntyre. 2006. Physical structure of lakes constrains epidemics in *Daphnia* populations. *Ecology* 87:1438–1444.
- Couture, S., D. Houle, and C. Gagnon. 2012. Increases of dissolved organic carbon in temperate and boreal lakes in Quebec, Canada. *Environmental Science and Pollution Research* 19:361–371.
- Debecker, S., R. Sommaruga, T. Maes, and R. Stoks. 2015. Larval UV exposure impairs adult immune function through a trade-off with larval investment in cuticular melanin. *Functional Ecology* 29:1292–1299.
- Decaestecker, E., C. Lefever, L. De Meester, and D. Ebert. 2004. Haunted by the past: evidence for dormant stage banks of microparasites and epibionts of *Daphnia*. *Limnology and Oceanography* 49:1355–1364.
- Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The relationship in lake communities between primary productivity and species richness. *Ecology* 81:2662–2679.
- Duffy, M. A. 2007. Selective predation, parasitism, and trophic cascades in a Bluegill–*Daphnia*–parasite system. *Oecologia* 153:453–460.
- Duffy, M. A., S. R. Hall, A. J. Tessier, and M. Huebner. 2005. Selective predators and their parasitized prey: are epidemics in zooplankton under top-down control? *Limnology and Oceanography* 50:412–420.
- Duffy, M. A., and K. K. Hunsberger. 2019. Infectivity is influenced by parasite spore age and exposure to freezing: Do shallow waters provide *Daphnia* a refuge from some parasites? *Journal of Plankton Research* 41:12–16.
- Duneau, D., P. Luijckx, F. Ben-Ami, C. Laforsch, and D. Ebert. 2011. Resolving the infection process reveals striking differences in the contribution of environment, genetics and phylogeny to host–parasite interactions. *BMC Biology* 9:11.
- Durif, C. M. F., D. M. Fields, H. I. Browman, S. D. Shema, J. R. Enoae, A. B. Skiftesvik, R. Bjelland, R. Sommaruga, and M. T. Arts. 2015. UV radiation changes algal stoichiometry but does not have cascading effects on a marine food chain. *Journal of Plankton Research* 37:1120–1136.
- Ebert, D. 2005. Some Parasites of *Daphnia*. *Ecology, epidemiology, and evolution of parasitism in Daphnia*, Bethesda, Maryland: National Center for Biotechnology Information (US).
- Ebert, D., P. Rainey, T. M. Embley, and D. Scholz. 1996. Development, life cycle, ultrastructure and phylogenetic position of *Pasteuria ramosa* Metchnikoff 1888: rediscovery of an obligate endoparasite of *Daphnia magna* Straus. *Philosophical Transactions of the Royal Society of London B* 351:1689–1701.
- Häder, D. P., H. D. Kumar, R. C. Smith, and R. C. Worrest. 2007. Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. *Photochemical & Photobiological Sciences* 6:267–285.
- Häder, D.-P., C. E. Williamson, S.-Å. Wängberg, M. Rautio, K. C. Rose, K. Gao, E. W. Helbling, R. P. Sinha, and R. Worrest. 2015. Effects of UV radiation on aquatic ecosystems and interactions with other environmental factors. *Photochemical & Photobiological Sciences* 14:108–126.
- Harrison, X. A., L. Donaldson, M. E. Correa-Cano, J. Evans, D. N. Fisher, C. E. D. Goodwin, B. S. Robinson, D. J. Hodgson, and R. Inger. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:1–32.
- Jacobs, J. F., G. J. M. Koper, and W. N. J. Ursem. 2007. UV protective coatings: a botanical approach. *Progress in Organic Coatings* 58:166–171.
- Kalff, J., and R. Knoechel. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. *Annual Review of Ecology and Systematics* 9:475–495.
- Karentz, D., F. S. McEuen, M. C. Land, and W. C. Dunlap. 1991. Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. *Marine Biology* 108:157–166.
- King, B. J., D. Hoefel, D. P. Daminato, S. Fanok, and P. T. Monis. 2008. Solar UV reduces *Cryptosporidium parvum* oocyst infectivity in environmental waters. *Journal of Applied Microbiology* 104:1311–1323.
- King, B. J., and Monis, P. T. 2007. Critical processes affecting *Cryptosporidium* oocyst survival in the environment. *Parasitology* 134 309–323.
- Kirk, J. T. O. 1993. Light and photosynthesis in aquatic ecosystems. Second edition. Cambridge University Press, Cambridge, UK.
- Kohn, T., M. J. Mattle, M. Minella, and D. Vione. 2016. A modeling approach to estimate the solar disinfection of viral indicator organisms in waste stabilization ponds and surface waters. *Water Research* 88:912–922.
- Kritzberg, E. S. 2017. Centennial-long trends of lake browning show major effect of afforestation. *Limnology and Oceanography Letters* 2:105–112.
- Kutz, S. J., E. P. Hoberg, J. Nishi, and L. Polley. 2002. Development of the muskox lungworm, *Umingmakstrongylus palikuukensis* (Protostrongylidae), in gastropods in the Arctic. *Canadian Journal of Zoology* 80:1977–1985.
- Lafferty, K. D., and R. D. Holt. 2003. How should environmental stress affect the population dynamics of disease? *Ecology Letters* 6:654–664.
- Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* 3:21–27.
- Larsen, S., T. Andersen, and D. O. Hessen. 2011. Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biology* 17:1186–1192.
- Laurion, I., M. Ventura, J. Catalan, R. Psenner, and R. Sommaruga. 2000. Attenuation of ultraviolet radiation in

- mountain lakes: factors controlling the among- and within-lake variability. *Limnology and Oceanography* 45:1274–1288.
- Leech, D. M., A. Padeletti, and C. E. Williamson. 2005. Zooplankton behavioral responses to solar UV radiation vary within and among lakes. *Journal of Plankton Research* 27:461–471.
- Long, J. A. 2019. jtools: Analysis and presentation of social scientific data. R package version 2.0.1. <https://cran.r-project.org/package=jtools>.
- Lowen, A. C., Mubareka, S., Steel, J., and Palese, P. 2007. Influenza virus transmission is dependent on relative humidity and temperature. *PLoS Pathogens* 3: 1470–1476.
- Manning, W. J., and A. V. Tiedemann. 1995. Climate change: potential effects of increased atmospheric carbon dioxide (CO₂), ozone (O₃), and ultraviolet-B (UV-B) radiation on plant diseases. *Environmental Pollution* 88:219–245.
- Metschnikoff, E. 1884. A disease of *Daphnia* caused by a yeast. A contribution to the theory of phagocytes as agents for attack on disease-causing organisms. *Archiv für pathologische Anatomie und Physiologie und für klinische Medizin* 96:177–195.
- Miller, C. J., Drasar, B. S. , and Feachem, R. G. 1982. Cholera and estuarine salinity in Calcutta and London. *The Lancet* 1216–1218.
- Monteith, D. T., et al. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* 450:537–540.
- Morris, D. P., H. Zagarese, C. E. Williamson, E. G. Balseiro, B. R. Hargreaves, B. Modenutti, R. Moeller, and C. Queimalinos. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography* 40:1381–1391.
- Nicholson, W. L., N. Munakata, G. Horneck, H. J. Melosh, and P. Setlow. 2000. Resistance of *Bacillus* endospores to extreme terrestrial and extraterrestrial environments. *Microbiology and Molecular Biology Reviews* 64:1092–2172.
- Roman, D.T., K. A. Novick, E. R. Brzostek, D. Dragoni, F. Rahman, and R. P. Phillips. 2015. The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought. *Oecologia*, 179: 641–654.
- Onofri, S., L. Selbmann, G. S. de Hoog, M. Grube, D. Barreca, S. Ruisi, and L. Zucconi. 2007. Evolution and adaptation of fungi at the boundaries of life. *Advances in Space Research* 40:1657–1664.
- Overholt, E. P., M. A. Duffy, M. P. Meeks, T. H. Leach, and C. E. Williamson. 2020. Light exposure decreases infectivity of the *Daphnia* parasite *Pasteuria ramosa*. *Journal of Plankton Research* 42:41–44.
- Overholt, E. P., S. R. Hall, C. E. Williamson, C. K. Meikle, M. A. Duffy, and C. E. Cáceres. 2012. Solar radiation decreases parasitism in *Daphnia*. *Ecology Letters* 15:47–54.
- Pietroock, M., and D. J. Marcogliese. 2003. Free-living endohelminth stages: at the mercy of environmental conditions. *Trends in Parasitology* 19:293–299.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. nlme: Linear and nonlinear mixed effects models. R package version 3.1-137. <https://CRAN.R-project.org/package=nlme>.
- R Core Team (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Read, D. J. 1968. Some aspects of the relationship between shade and fungal pathogenicity in an epidemic disease of pines. *New Phytologist* 67:39–48.
- Rhode, S. C., M. Pawlowski, and R. Tollrian. 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature* 412:69–72.
- Roland, J., and W. J. Kaupp. 1995. Reduced transmission of forest tent caterpillar (Lepidoptera: Lasiocampidae) nuclear polyhedrosis virus at the forest edge. *Environmental Entomology* 24:1175–1178.
- Roy, S. 2000. Strategies for the minimization of UV-induced damage. Pages 177–201 in S. De Mora and M. Serge Demers, editors. *The effects of UV radiation in the marine environment*. Cambridge University Press, Cambridge, UK.
- Ruelas, D. S., D. Karentz, and J. T. Sullivan. 2007. Sublethal effects of ultraviolet B radiation on miracidia and sporocysts of *Schistosoma mansoni*: intramolluscan development, infectivity, and photoreactivation. *Journal of Parasitology* 93:1303–1310.
- Ruisi, S., D. Barreca, L. Selbmann, L. Zucconi, and S. Onofri. 2007. Fungi in Antarctica. *Reviews in Environmental Science and Biotechnology* 6:127–141.
- Saebelfeld, M., L. Mínguez, J. Griebel, M. O. Gessner, and J. Wolinska. 2017. Humic dissolved organic carbon drives oxidative stress and severe fitness impairments in *Daphnia*. *Aquatic Toxicology* 182:31–38.
- Sánchez, K. F., N. Huntley, M. A. Duffy, and M. D. Hunter. 2019. Toxins or medicines? Phytoplankton diets mediate host and parasite fitness in a freshwater system. *Proceedings of the Royal Society B* 286:1–10.
- Schindler, D. W., S. R. Carpenter, S. C. Chapra, R. E. Hecky, and D. M. Orihel. 2016. Reducing phosphorus to curb lake eutrophication is a success. *Environmental Science and Technology* 50:8923–8929.
- Setlow, P., and L. Li. 2015. Photochemistry and photobiology of the spore photoproduct: a fifty year journey. *Photochemical & Photobiological Sciences* 91:1263–1290.
- Shocket, M. S., A. T. Strauss, J. L. Hite, M. Šljivar, D. J. Civitello, M. A. Duffy, C. E. Cáceres, and S. R. Hall. 2018. Temperature drives epidemics in a zooplankton–fungus disease system: a trait-driven approach points to transmission via host foraging. *American Naturalist* 191:435–451.
- Sinha, R. P., and D. P. Häder. 2002. UV-induced DNA damage and repair: a review. *Photochemical & Photobiological Sciences* 1:225–236.
- Solomon, C. T., et al. 2015. Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: current knowledge and future challenges. *Ecosystems* 18:376–389.
- Sommer, U. 1985. Seasonal succession of phytoplankton in Lake Constance. *BioScience* 35:351–357.
- Storz, U. C., and R. J. Paul. 1998. Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. *Journal of Comparative Physiology A* 183:709–717.
- Strock, K. E., S. J. Nelson, J. S. Kahl, J. E. Saros, and W. H. McDowell. 2014. Decadal trends reveal recent acceleration in the rate of recovery from acidification in the northeastern U.S. *Environmental Science and Technology* 48:4681–4689.
- Strock, K. E., J. E. Saros, S. J. Nelson, S. D. Birkel, J. S. Kahl, and W. H. McDowell. 2016. Extreme weather years drive episodic changes in lake chemistry: implications for recovery from sulfate deposition and long-term trends in dissolved organic carbon. *Biogeochemistry* 127:353–365.
- Studer, A., M. D. Lamare, and R. Poulin. 2012. Effects of ultraviolet radiation on the transmission process of an intertidal trematode parasite. *Parasitology* 139:537–546.
- Tucker, A. J., and C. E. Williamson. 2011. Lakes in a new light: indirect effects of ultraviolet radiation. *Freshwater Reviews* 4:115–134.
- van Dijk, J., M. D. E. de Louw, L. P. A. Kalis, and E. R. Morgan. 2009. Ultraviolet light increases mortality of nematode larvae and can explain patterns of larval availability at pasture. *International Journal for Parasitology* 39:1151–1156.

- Villarreal, P., M. Carrasco, S. Barahona, J. Alcaíno, V. Cifuentes, and M. Baeza. 2016. Tolerance to ultraviolet radiation of psychrotolerant yeasts and analysis of their carotenoid, mycosporine, and ergosterol content. *Current Microbiology* 72:94–101.
- Weyhenmeyer, G. A., R. A. Müller, M. Norman, and L. J. Tranvik. 2016. Sensitivity of freshwaters to browning in response to future climate change. *Climatic Change* 134:225–239.
- Williamson, C. E., J. M. Fischer, S. M. Bollens, E. P. Overholt, and J. K. Breckenridge. 2011. Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnology and Oceanography* 56:1603–1623.
- Williamson, C. E., S. Madronich, A. Lal, R. G. Zepp, R. M. Lucas, E. P. Overholt, K. C. Rose, S. G. Schladow, and J. Lee-Taylor. 2017. Climate change-induced increases in precipitation are reducing the potential for solar ultraviolet radiation to inactivate pathogens in surface waters. *Scientific Reports* 7:1–38.
- Williamson, C. E., P. J. Neale, G. Gard, H. J. De Lange, and B. R. Hargreaves. 2001. Beneficial and detrimental effects of UV on aquatic organisms: implications of spectral variation. *Ecological Applications* 11:1843–1857.
- Williamson, C. E., P. J. Neale, S. Hylander, K. C. Rose, F. L. Figueroa, S. A. Robinson, D. P. Häder, S.-A. Wängberg, and R. C. Worrest. 2019. The interactive effects of stratospheric ozone depletion, UV radiation, and climate change on aquatic ecosystems. *Photochemical and Photobiological Sciences* 18:717–746.
- Xenopoulos, M. A., D. M. Lodge, J. Frentress, T. A. Kreps, S. D. Bridgman, E. Grossman, and C. J. Jackson. 2003. Regional comparisons of watershed determinants of dissolved organic carbon in temperate lakes from the upper Great Lakes region and selected regions globally. *Limnology and Oceanography* 48:2321–2334.
- Yaun, B. R., S. S. Sumner, J. D. Eifert, and J. E. Marcy. 2004. Inhibition of pathogens on fresh produce by ultraviolet energy. *International Journal of Food Microbiology* 90:1–8.
- Zellmer, I. D. 1995. UV-B-tolerance of alpine and arctic *Daphnia*. *Hydrobiologia* 307:153–159.

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.w3r2280nk>