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**Running head:** Lighter lakes restrict epidemics

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

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## 27 **ABSTRACT**

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

43

44 **Key Words:** light, DOM, *Daphnia*, parasite, lakes, climate change

45

## 46 **INTRODUCTION**

47 Free-living stages of parasites often must survive wide-ranging environmental conditions  
48 in nature while awaiting encounters with new hosts. Since outside-of-host environments often  
49 vary more extremely than within-host conditions, this free-living stage can pose challenges for  
50 parasites. Transmission stages of some parasites can be well-protected from environmental  
51 conditions (e.g., helminths: Pietrock and Marcogliese 2003; *Cryptosporidium*: King & Monis  
52 2007). However, for many parasites with environmental stages, abiotic factors can harm their  
53 fitness, e.g., low temperatures (lungworm: Kutz et al. 2002), high humidity (influenza: Lowen et  
54 al. 2007), and low salinity (cholera: Miller et al. 1982). If changing climatic conditions alter  
55 these abiotic constraints on parasite fitness, climate change could alter the timing and magnitude

56 of disease epidemics (Williamson et al. 2017).

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

71 Several ecosystem features affect the light environment. Exposure to potentially harmful  
72 wavelengths of sunlight in natural ecosystems is largely controlled by sun angle (latitude, time of  
73 day, time of year) and cloud cover. In aquatic environments, those features govern incident light  
74 to the water surface. Exposure to light in the water column then becomes depth-dependent, as  
75 absorption means that deeper waters experience less light. Notably, light is absorbed and  
76 scattered by dissolved and particulate compounds (including algae). Some of these compounds,  
77 especially dissolved organic matter (DOM), selectively absorb UV radiation (Kirk 1994). DOM  
78 therefore protects organisms within lakes from these potentially more harmful shorter  
79 wavelengths. The concentrations of compounds like DOM, phytoplankton, etc., vary both  
80 through time (Kalff and Knoechel 1978, Sommer 1985, Couture et al. 2012) and across a  
81 landscape (Morris et al. 1995, Dodson et al. 2000, Laurion et al. 2000, Xenopoulos et al. 2003).  
82 Notably, many lakes are becoming darker due to human activities (Monteith et al. 2007, Larsen  
83 et al. 2011, Strock et al. 2014, 2016, Solomon et al. 2015, Schindler et al. 2016, Weyhenmeyer et  
84 al. 2016, Kritzberg 2017).

85 Changes to the light environment may alter disease dynamics in lakes by removing light  
86 as a constraint on environmentally transmitted parasites (Williamson et al. 2017). To evaluate

87 this potential, we examined light effects on fitness of free-living stages of parasites and natural  
88 outbreaks along light gradients. In the focal system, *Daphnia* hosts migrate deep into the water  
89 column during the day (Lampert 1989, Williamson et al. 2011), greatly reducing their UV  
90 exposure (Storz and Paul 1998, Rhode et al. 2001, Leech et al. 2005). However, the infective  
91 propagules (hereafter: spores) of the two focal parasites, *Pasteuria ramosa* and *Metschnikowia*  
92 *bicuspidata* (hereafter: *Pasteuria* and *Metschnikowia*) cannot swim. Thus, they cannot  
93 behaviorally escape light exposure. While both parasites can reach epidemic prevalence in  
94 *Daphnia* populations in autumn (Cáceres et al. 2006, Auld et al. 2014), both are sensitive to UV  
95 and photosynthetically active radiation (PAR) (Overholt et al. 2012, 2020). Though *Daphnia*  
96 survival can be reduced by high levels of UV radiation when exposed (Williamson et al. 2001,  
97 Overholt et al. 2012), low levels of UV radiation do not impact host susceptibility to  
98 *Metschnikowia*, and *Metschnikowia* is much more sensitive to radiation than is *Daphnia*  
99 (Overholt et al. 2012). The present study extends prior work (Overholt et al. 2012, 2020), which  
100 focused on a single parasite at a time. In this study, we ask whether light shapes the relative  
101 dynamics in multi-parasite systems. To evaluate relative sensitivity of these parasites to light  
102 over the epidemic season, we experimentally incubated parasite spores in lakes in July, August,  
103 and November (i.e., decreasing incident light across the epidemic season) in light exposed vials  
104 (or covered vials as a control) and then used them to infect hosts in the lab, quantifying spore  
105 infectivity. Then, with field survey data, we examined the relationship between lake transparency  
106 and parasite dynamics. We expected that epidemics would start later (i.e., as the light constraint  
107 waned autumnally) and remain smaller in more transparent lakes.

108

## 109 **METHODS**

### 110 **Hosts and Parasites**

111 The host, *Daphnia dentifera*, is common in Midwestern (USA) lakes. It is susceptible to  
112 parasites including *Pasteuria ramosa* (a bacterium) and *Metschnikowia bicuspidata* (a fungus).  
113 Both parasites share similar infection mechanisms and life cycles. For instance, both infect their  
114 hosts by penetrating the digestive tract after being accidentally consumed during host feeding  
115 (Metschnikoff 1884; Duneau et al. 2011). Then, both replicate in the hemolymph of hosts, filling  
116 host bodies with spores (Ebert 2005). Most important for this study, upon host death those spores  
117 are released into the water column where they can be consumed by a new host, completing the

118 infection cycle (Metschnikoff 1884; Ebert 2005). In laboratory conditions, spores of both  
119 parasites are long-lived relative to the length of an epidemic (Duffy and Hunsberger 2019), but,  
120 in stratified lakes, they may sink out of the water column to lake sediments unless conditions are  
121 turbulent. It is while the parasite is in the water column during environmental dispersal that light  
122 could most strongly impinge on epidemics via direct effects on spores.

123

## 124 **Lake Transparency Measurements and Metrics**

125 In order to quantify light exposure for parasites in the incubation experiment, we  
126 measured within-lake light attenuation and surface-level ambient light during incubations.  
127 Within-lake attenuation of both UV (320 nm) and PAR (400-700 nm) was measured directly  
128 (BIC 2104, Biospherical Instruments; Appendix S1: Section S1). Each metric was converted to a  
129 percent of incident light remaining at incubation depth (0.5 m and 2 m). Surface-level incident  
130 320 nm UV and PAR was integrated over 3 minute time intervals by a radiometer (Model  
131 2104RL, Biospherical Instruments) deployed at the Greene Sullivan State Forest ranger station  
132 located within 10 miles of all experimental lakes (Appendix S1: Section S1, Table S1).  
133 Cumulative surface level incident UV and PAR are documented for each incubation in Figure 1  
134 and in Appendix S1: Table S1. We multiplied percent incident light at incubation depth and  
135 surface level incident light measurements to obtain within-lake light exposure for 320 nm UV  
136 and PAR separately (Appendix S1: Section S3).

137 For the field survey we indexed lake transparency as the depth at which 1% of incident  
138 320 nm UV remained. To calculate this index, we measured the absorbance of 320 nm UV light  
139 of filtered lake water samples (using GF/F filtrate from lake epilimnia and a Shimadzu UV/  
140 Visible UV-1650 PC spectrophotometer). With these absorbance values, we estimated light  
141 penetration in the water column (with Beer-Lambert law; Appendix S1: Section S1). More  
142 transparent (lighter) lakes have deeper values for 1% 320 nm UV remaining (larger scaled  
143 transparency values). Attenuation of 320 nm UV and of PAR are correlated in our study lakes  
144 ( $r^2=0.80$ ,  $p<0.001$ ). Thus, darker lakes have both less UV and less PAR. To characterize incident  
145 light, we calculated daily maximum short wave radiation from the AmeriFlux site at Morgan  
146 Monroe State Forest, Indiana (60 miles from study lakes; Novick and Phillips 1999-present).  
147 These data provide a visual descriptor of light throughout autumn and among years.

148

149 **Spore Incubation Methods**

150 We incubated spore slurries of each parasite in lakes to assess their infectivity after exposure to  
151 ambient sunlight *in situ* in July (20-25), August (15-20), and November (31 Oct-5 Nov 2016).  
152 We selected five lakes along a gradient of water transparency: Airline, Canvasback, Beaver  
153 Dam, Goodman, and Midland lakes (Appendix S1: Section S1, Table S1). Six quartz vials filled  
154 with *Pasteuria* or *Metschnikowia* spore slurries were suspended at 0.5 m and 2 m depths in each  
155 lake, for a total of 24 vials per lake (6 per parasite per depth). Half of these vials were covered in  
156 dark plastic ('dark treatment'); the others were left uncovered, and hence exposed to ambient  
157 light at depth (i.e., PAR + UV; 'light treatment'; see Appendix S1: Section S2 for additional  
158 details). Parasite spore slurries were composed of infected lab animals that were ground in lake  
159 water to release spores. These slurries were pipetted into vials such that each *Pasteuria* vial  
160 contained 300,000 spores in each incubation month and each *Metschnikowia* vial contained  
161 15,000 spores in the July incubation and 37,500 spores in August and November incubations.

162 After the incubation period, incubated spore slurries as well as algal food  
163 (*Ankistrodesmus falcatus*) were added to 150 mL filtered lake water, yielding spore  
164 concentrations of 2,000 spores/mL of *Pasteuria* and 100 spores/mL of *Metschnikowia* in July  
165 and 250 spores/mL of *Metschnikowia* in August and November. *Metschnikowia* spore dose was  
166 increased in August and November due to low infection levels in the control treatment in July,  
167 with both 100 and 250 spores/mL being within the range typically used in lab experiments  
168 (Shocket et al. 2018, Duffy and Hunsberger 2019). This water-algae-spore mixture was  
169 distributed among either ten (July and August incubations) or eight (November) 15 mL  
170 centrifuge tubes. For both parasites, we placed 3-4 day old, individual *Daphnia* of a clone  
171 ('Mid37') that is susceptible to both parasites into the tubes. After 24 hours of exposure at 20° C,  
172 we moved *Daphnia* to 50 mL tubes. We maintained each individually (still at 20° C) with daily  
173 feeding and water changes every other day until visual diagnosis of infection (Appendix S1:  
174 Section S2).

175 We used generalized linear mixed models (GLMMs) with binomial error structures to test  
176 the effects of light treatment (light-exposed or covered vials), depth, and month on host infection  
177 status. The first model evaluated which parasite was more sensitive to light. Hence, only parasite,  
178 light treatment, and the interaction were included as fixed effects with a lake by month  
179 interaction as a random effect. Then, we evaluated each parasite separately. The second set of

180 models fit light treatment, depth, month, and their interactions as fixed effects for each parasite  
181 (retaining the lake by month interaction as a random effect). Finally, in a third set of models, data  
182 were analyzed for each month separately with otherwise similar fixed and random effects. All  
183 significant interaction terms were included that still allowed for model convergence. Note that  
184 for these analyses, lake-specific light conditions were not included. An additional analysis  
185 evaluated the effects of light exposure in lakes on relative infectivity of light-exposed spores as  
186 compared with those in covered vials (Appendix S1: Section S3). All statistics were performed  
187 in R Version 3.5.3 (R Development Core Team). GLMMs were performed with the lme4  
188 package (Bates et al. 2015).

189

## 190 **Field Survey**

191 We used a field survey to link light sensitivity of parasites to the timing and size of  
192 parasite outbreaks in lakes. We sampled 37 lakes in south central Indiana (Greene and Sullivan  
193 counties) approximately every two weeks, August - November, during 2014-2016 (Appendix S1:  
194 Section S4); these lakes all stratify during summer, but stratification breaks down in early in fall  
195 in some of the shallower lakes. Notably, this is substantially more lakes and years than in a  
196 related earlier study: the Overholt et al. (2012) study focused on 18 lakes in a single year. At  
197 each sample date, we pooled three vertical plankton tows (each from the bottom of the lake up  
198 through the surface); each of the tows was collected at least 25 m apart with a Wisconsin net (13  
199 cm diameter, 153 micron mesh). From those tows, we visually diagnosed live *D. dentifera* from  
200 subsamples of the entire collection for late-stage infection using a dissecting microscope (40-  
201 50X). We define 'outbreak size' as the maximum prevalence of infection during the season.  
202 Epidemics ('large' outbreaks) 'started' on the first date at which infection prevalence reached  
203 and remained above 1% for at least one more visit (Duffy et al. 2005). 'Small' outbreaks did not  
204 maintain prevalence above 1% for more than one visit.

205 We compared start dates of epidemics between parasites with a linear mixed effects  
206 model. In this model, epidemic start date was the response variable, parasite identity was a fixed  
207 effect, and year and lake were random effects (nlme package in R; Pinheiro et al. 2018). A paired  
208 t-test was also used to compare start dates of parasites in lake-years where epidemics of both  
209 parasites occurred. This smaller subset of lakes controls for within-lake factors that could also  
210 influence epidemic start dates. For each parasite, we also fit binomial generalized linear mixed

211 effects models to link our index of lake transparency (depth of 1% 320 nm UV remaining) to  
212 maximum infection prevalence (lme4 package; Bates et al. 2015). In global models, maximum  
213 prevalence was predicted by transparency, epidemic start date, lake depth, mean host density,  
214 mean chlorophyll concentrations, and year as fixed effects and an observation level random  
215 effect to mitigate overdispersion (Harrison et al. 2018). All fixed effects except year were  
216 centered and scaled. Results from the model with the lowest AIC are presented in the text with  
217 predicted effects of fixed effects displayed with the jtools package in R (Long 2019). Effects of  
218 the predictors were found to be qualitatively similar to their effects in the global model and  
219 various subsets of it (Appendix S1: Section S5). To evaluate whether high transparency inhibited  
220 epidemics ('large' outbreaks; see above), we used a t-test to compare the transparency of lakes  
221 with epidemics to lakes with small or non-existent outbreaks.

222

## 223 RESULTS

### 224 Spore Incubations

225 Spores of both parasites were less infective after incubation in ambient light, but the  
226 infectivity of *Metschnikowia* was reduced more. This differential sensitivity to light appeared as  
227 a significant interaction between parasite and light treatment (parasite x light:  $z=2.71$ ,  $P=0.007$ ).  
228 Additionally, infectivity of *Metschnikowia* was still reduced by incident light in late summer  
229 (Aug) and fall (Nov; Figure 1D & F). In contrast, the impact of incident light on *Pasteuria*  
230 decreased as the season progressed (Figure 1 left panels). More specifically, compared to July  
231 incubations, light-exposed *Pasteuria* spores infected a greater proportion of hosts in August  
232 ( $z=5.42$ ,  $P<0.001$ ; compare Figure 1A & C) and November ( $z=6.76$ ,  $P<0.001$ ; compare Figure  
233 1A & E). The diminishing seasonal impact of light on *Pasteuria* also manifested in the separate  
234 analyses of months. In July, spores exposed to ambient light were less infective (light:  $z=-8.26$ ,  
235  $P<0.001$ ), especially at shallower depths where light was greater (light x depth:  $z=5.61$ ,  $P<0.001$ ;  
236 Figure 1A). Though incident light declined in August (Figure 1G), the main effect of light  
237 remained ( $z=-3.41$ ,  $P<0.001$ ; Figure 1C). However, in still darker November, light no longer  
238 constrained success of *Pasteuria* (light:  $z=-1.00$ ,  $P=0.318$ ; light x depth:  $z=1.13$ ,  $P=0.259$ ; Figure  
239 1E). Thus, exposure to ambient light reduced infectivity of *Pasteuria* spores in summer, but by  
240 late autumn, this inhibitory effect on *Pasteuria* disappeared.

241 The fungal parasite *Metschnikowia* was more sensitive to light. Light damaged spores



242 throughout the epidemic season (light:  $z=-4.42$ ,  $P<0.001$ ), but depth provided some protection  
243 from light damage (light x depth:  $z=2.50$ ,  $P=0.013$ ). Both August ( $z=1.96$ ,  $P=0.050$ ; Figure 1D)  
244 and November ( $z=3.27$ ,  $P=0.001$ ; Figure 1F) showed higher overall proportion infected hosts  
245 compared to July when the spore dose was lower (Figure 1B; see Methods). However, light  
246 remained a strong constraint throughout autumn: even in later, darker months, spores from light-  
247 exposed treatments were less infective than spores from covered treatments (Figure 1B, D, & F).  
248 In each month analyzed separately, spores exposed to light infected a smaller proportion of hosts  
249 in July ( $z=-1.99$ ,  $P=0.047$ ; Figure 1B), August ( $z=-3.67$ ,  $P<0.001$ ; Figure 1D) and November  
250 ( $z=-4.00$ ,  $P<0.001$ ; Figure 1F); no depth or depth x light interactions were significant likely  
251 because we did not have the statistical power to detect these effects with the data subsetted by  
252 month. Overall, unlike for *Pasteuria*, light continued to significantly impact the infectivity of  
253 *Metschnikowia* spores well into autumn.

254

### 255 **Field Survey**

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

265 Since both parasites were sensitive to light, we tested two hypotheses. First, we expected  
266 epidemics (larger outbreaks) of a given parasite to start later in ‘lighter lakes’ (i.e., more  
267 transparent, with deeper light penetration). In these lakes, higher light levels should more  
268 effectively kill spores for a longer portion of the year. Second, outbreaks should remain smaller  
269 in lighter lakes, due to direct mortality effects on spores. For *Pasteuria*, too few outbreaks  
270 qualified as epidemics to test for the effect of start date on epidemic size. However, less  
271 transparent lakes had larger outbreaks ( $LRT=30.95$ ,  $P<0.001$ ; Figure 3A). Furthermore, lakes  
272 with *Pasteuria* epidemics were less transparent than those with just minor outbreaks ( $t=-4.92$ ,

273 P<0.001; Figure 3A). Small outbreaks in general may have made it more difficult to detect  
274 effects of the other covariates that were originally included in the global model (Appendix S1:  
275 Section S5).

276 For *Metschnikowia*, though epidemics did not start earlier in darker lakes (F=0.95,  
277 P=0.34), darker lakes had larger epidemics (LRT=6.52, P=0.011, Figure 3B). Epidemic size was  
278 also associated with epidemic start date (earlier starting epidemics grew larger: LRT=11.36,  
279 P<0.001, Figure 3C), lake depth (deeper lakes had larger epidemics: LRT=7.91, P=0.005, Figure  
280 3D), and host density (lakes with higher host densities had larger epidemics: LRT=8.78,  
281 P=0.003, Figure 3E).

282

## 283 DISCUSSION

284 Light impacts many environmentally transmitted parasites. In some cases, light damages  
285 free living stages. In these cases, waters darkened by human activities could unleash larger  
286 disease outbreaks. To better understand this possibility, we evaluated light effects on parasite  
287 outbreaks in Midwestern lakes with an incubation experiment and a field study. Both parasites  
288 responded sensitively to ambient light conditions in summer (July). For the more sensitive  
289 *Metschnikowia*, these effects persisted even into November. Consistent with this differential  
290 sensitivity, we found that *Pasteuria* epidemics began earlier in the fall (when light levels begin to  
291 decrease). Furthermore, transparent lakes had smaller outbreaks of both parasites.

292 In the incubation experiment, light reduced the infectivity of parasite spores (especially  
293 *Metschnikowia*). We did not separate UV from PAR effects here, but both likely reduced spore  
294 infectivity. UV is typically more damaging, interfering with replication and transcription of DNA  
295 (Sinha and Häder 2002). However, despite only shallow penetration of UV (see Appendix S1:  
296 Figure S2), spores still suffered reduced infectivity when incubated at 2 m depth, and  
297 *Metschnikowia* experienced reduced infectivity even in late autumn (when incident UV was  
298 negligible). Thus, PAR likely damaged spores too, which is consistent with evidence from  
299 laboratory experiments on *Metschnikowia* and *Pasteuria* (Overholt et al. 2012, 2020).  
300 Differential sensitivity among parasites may stem from differences in protective or repair  
301 mechanisms. For instance, *Pasteuria* resides in the *Bacillus* clade (Ebert et al. 1996) where  
302 species resist UV through several mechanisms (Nicholson et al. 2000, Setlow and Li 2015).  
303 Some fungi tolerate UV well (Onofri et al. 2007) due to protective pigments, etc. (Ruishi 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 (due to 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),

335 *Vibrio cholerae* (Berney et al. 2006)). By reducing light damage to pathogens, browning waters  
336 may unleash epidemics of aquatic parasites infecting wildlife and humans (Williamson et al.  
337 2017). Light also affects disease in terrestrial systems. For example, transmission of a virus of  
338 forest tent caterpillars was reduced in lighter environments (e.g., near edges and in patchy  
339 fragments) relative to darker interiors of forests (Roland and Kaupp 1995). Corsican Pine also  
340 showed higher rates of a fungal disease on north facing (darker) slopes, and in an artificial  
341 shading experiment (Read 1968). Furthermore, light might be shaping patterns of disease even  
342 within individuals, since most fungal diseases occur on protected parts of plants, like the  
343 undersides of leaves (Manning and Tiedemann 1995). Hence, habitat-driven light environment  
344 may shape disease in both aquatic and terrestrial systems.

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

353

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362

## 363 **SUPPORTING INFORMATION**

364 Additional supporting information may be found online at: [link to be added in production].

365

366 **DATA AVAILABILITY**

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

368

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576

### 577 **Figure Legends.**

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

587 correspond to cumulative differences in surface level UV and PAR along lakes.

588

589 **Figure 2:** Epidemics of the less light-sensitive bacterium *Pasteuria* started earlier than those of  
590 the more sensitive fungus, *Metschnikowia*. (A) Maximum short wave radiation decreases  
591 autumnally near the study lakes (Morgan Monroe State Forest, IN; Novick and Phillips 1999-  
592 present). Loess trendlines accompany data from each year of the survey (2014, 2015, and 2016).  
593 Epidemics of *Pasteuria* started earlier in (B) lakes that showed epidemics of either parasite and  
594 in (C) lakes with epidemics of both in the same year. Dashed lines denote the first day of August  
595 (lowest), September, October, and November (highest day, as labeled).

596

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

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Figure 1.

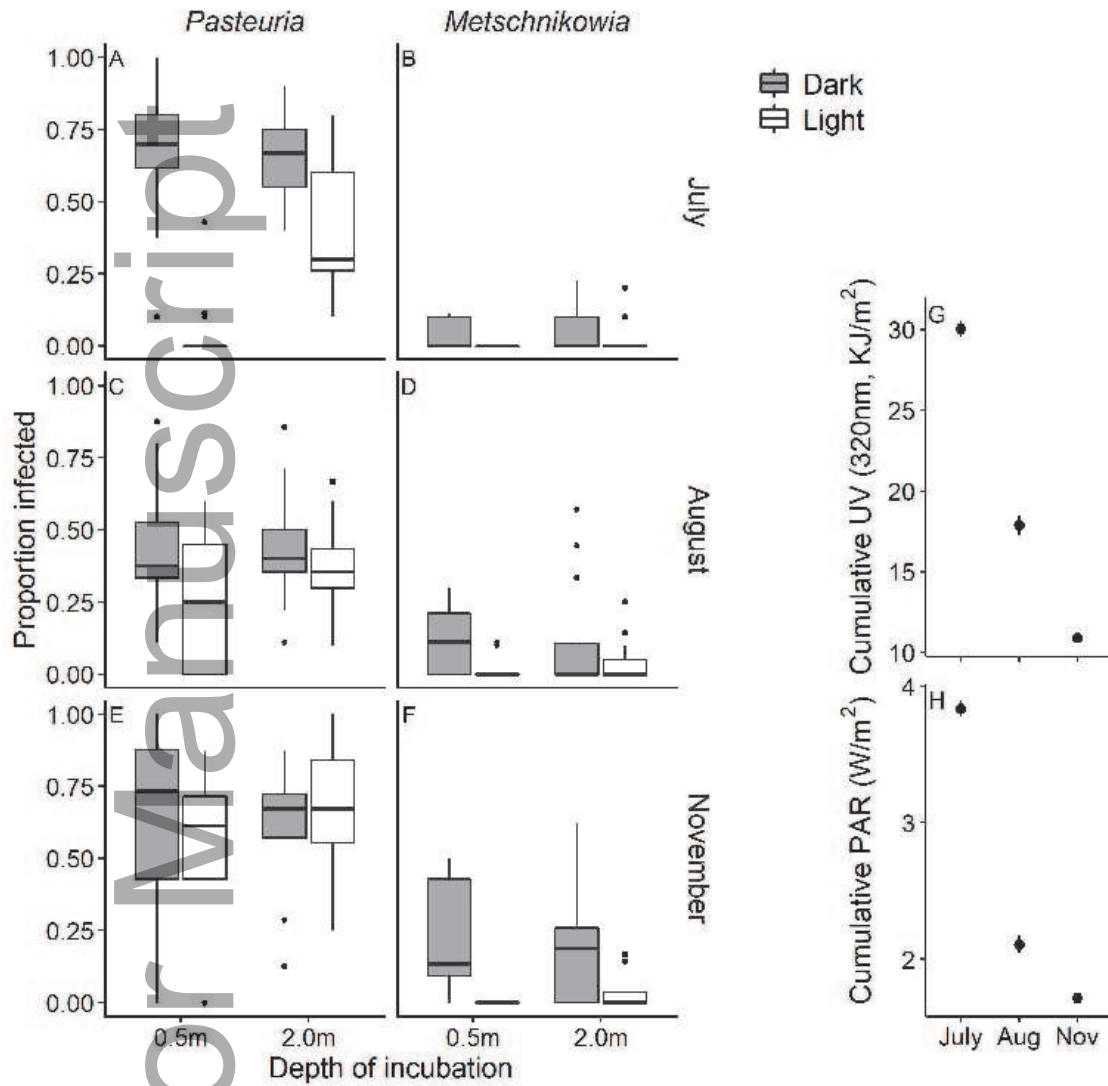
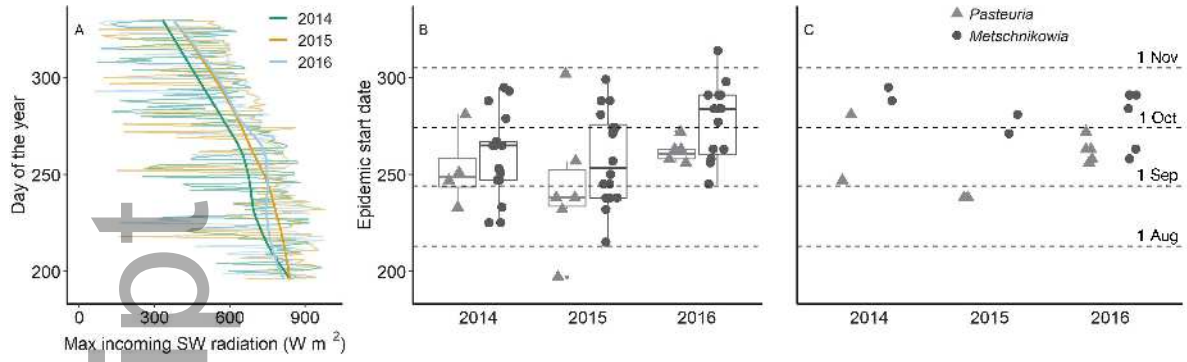


Figure 2.



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Figure 3.

