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Can climate warming save *Daphnia* from parasites? Reduced parasite prevalence in *Daphnia* populations from artificially heated lakes

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Abstract

Climate warming might modify infection outcomes and it has been proposed that temperature increase will result in a "sicker world." We tested this hypothesis by comparing the prevalence of infection in a common freshwater host–parasite system (crustacean *Daphnia* infected with the ichthyosporean pathogen *Caullerya mesnili*) between five artificially heated lakes and four nearby non-heated control lakes. The heated lakes, which receive warm water from two power plants, have experienced an elevation in water temperature of ca. 3–4°C for the last 60 yr. Analyses of 5 yr of field data revealed that *Daphnia* communities from heated lakes had lower parasite prevalence than communities from control sites. To disentangle a possible direct detrimental effect of elevated temperature on the parasite from differences in baseline levels of host resistance, we compared infection susceptibility between *Daphnia* clones isolated from heated and control lakes, under laboratory conditions at two different temperatures. *Daphnia* from heated lakes were less susceptible to infection than clones from control lakes, while experimental temperature did not affect infection outcome. The data did not confirm the "warmer hence sicker world" scenario. Instead, it seems that indirect effects of temperature elevation (via shifts in lake hydrology) may restrict its spread into heated lakes. Then, local adaptation to the host from control lakes further inhibits re-establishment of the parasite from control to heated lakes. Our results underline the context-dependency of the impact of temperature increase on host–parasite interactions.

Climate warming significantly disturbs the performance of aquatic species (Moss et al. 2009; Doney et al. 2011; De Senerpont Domis et al. 2013). Thermal conditions can alter the development, reproduction (Atkinson 1994; Kingsolver and Huey 2008), behavior, and distribution (Świerzowski and Godlewska 2001; Parmesan 2006; Bellard et al. 2012) of organisms, all of which may strongly impact the infection-related traits of host and pathogen. More directly, temperature has been shown to modify the infectivity and virulence of parasites as well as host susceptibility (Blanford et al. 2003; Kirk et al. 2018) and the frequency of encounters between host and parasite (Shocket et al. 2018*a*,*b*), thus changing infection outcomes especially for parasites with ectothermic hosts or vectors (Altizer et al. 2013; Velásquez et al. 2018; Price et al. 2019). There is a general concern that climate change will be advantageous for certain pathogens due to disproportionately increased development and replication rates as well as enhanced transmission (the "warmer hence sicker world" hypothesis; Brooks and Hoberg 2007; Marcogliese 2008; Altizer et al. 2013), but this hypothesis remains controversial. If anything, most studies indicate that the influence of temperature on disease dynamics is rarely straightforward and rather context dependent (Lafferty et al. 2004; Duffy et al. 2012; Lafferty and Mordecai 2016). There is a substantial body of evidence that temperature increases can in fact reduce disease prevalence (Berger et al. 2004; Raffel et al. 2010; Gehman et al. 2018). Available mechanistic models indicate that thermal conditions can have positive or negative impacts

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Additional Supporting Information may be found in the online version of this article.

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on disease, depending on the focal organisms (Molnár et al. 2013). Moreover, the outcome of most host–parasite interactions is also shaped by components of the environment other than temperature, for example, host nutrition, light conditions, or presence of a third species (Wolinska and King 2009; Pike et al. 2019; Shaw et al. 2020). Such additional variables might interact directly or indirectly with temperature, making predictions of host–parasite dynamics in the face of climate change even more challenging (Hall et al. 2006).

Elevated temperatures can be relatively easy to simulate in the laboratory, but the full complexity of an ecosystem usually cannot be reproduced in experimental settings. Case and field studies are thus highly valuable for verification of experimental findings and for drawing more general conclusions. However, field studies usually preclude the application of temperature increases to simulate anticipated conditions under global warming. To test relevant temperature conditions (i.e., corresponding to climate change scenarios) without compromising ecological realism (which is often the case in fully controlled but simplified laboratory manipulations), we studied the effect of global warming on host–parasite dynamics using a system of natural lakes that have been artificially heated for six decades. These lakes have been receiving warm water from an adjacent system of power plants resulting in an average temperature increase of ca. 3–4°C, corresponding well to climate change forecasts for the coming decades (Pörtner et al. 2019). Importantly, four non-heated lakes lie in close proximity and were used as control sites.

Both heated and control lakes are inhabited by cladocerans of the genus *Daphnia*, which are the most abundant planktonic herbivores in standing freshwater bodies like lakes and ponds and link primary producers (phytoplankton) with higher levels of the food web (e.g., fish, insect larvae). *Daphnia* populations are infected frequently by various parasite species (Ebert 2005; Wolinska et al. 2009), and parasite-induced changes in *Daphnia* abundances can impact the entire food web: parasites can decimate *Daphnia* populations, releasing phytoplankton from their control (Duffy 2007) or increasing the vulnerability of infected *Daphnia* to fish predation (Duffy et al. 2005). In our heated and control lake system, the most abundant parasite of *Daphnia* populations is *Caullerya mesnili*. This ichthyosporean parasite (Lohr et al. 2010; Lu et al. 2020), hereafter referred to as *Caullerya*, has frequently been reported to cause regular epidemics across various *Daphnia* populations, with up to 40% of the entire host population being infected at a given time (Wolinska et al. 2007, 2011; Turko et al. 2018). The parasite infects gut epithelium cells of its *Daphnia* host and is transmitted horizontally: spores of *Caullerya* released from one *Daphnia* are taken up directly by neighboring individuals, leading to a rapidly spreading infection (Bittner et al. 2002; Lohr et al. 2010). *Caullerya* infections result in host castration and early mortality (Wolinska et al. 2006, 2007). Parasite infectivity varies among host genotypes and taxa (Wolinska et al. 2006; Schoebel et al. 2010); therefore *Caullerya* is an important driver of genetic structure in host populations, being involved in a host–parasite coevolutionary arms race (Turko et al. 2018).

Using a system of heated and nearby non-heated (control) lakes, we tested the "warmer hence sicker world" scenario by comparing the prevalence of the parasite *Caullerya* among *Daphnia longispina* complex communities inhabiting these two types of lakes. Water temperature increase is expected to have direct effects on the investigated organisms, but also induce a multitude of other effects with possible indirect consequences; for example, alteration in ice phenology, changes inflicted on different trophic levels of the food web (like increased growth of algae—the food base for the host, or stronger predation on the host), or altered water transparency, to name a few (Adrian et al. 2009). We expected to observe a relationship between the thermal regime of the investigated lakes and the infection prevalence, but we also wanted to parse the sole effect of temperature from possible indirect effects of warming. Hence, we designed the experiment testing how successfully *Caullerya* establishes infection on *Daphnia* clones isolated from the heated and control lakes, depending on experimental temperature. The experiment aimed to investigate whether the observed difference in parasite prevalence between heated and control lakes could be attributed to the direct impact of temperature on parasite infectivity. Alternatively, varying baseline levels of host resistance, or other environmental factors could play a role.

Methods

Study sites and field sampling

Prevalence of *Caullerya* was investigated in five heated lakes (Gosławskie, Licheńskie, Pątnowskie, Ślesińskie, and Mikorzyńskie) and four non-heated (control) lakes (Budzisławskie, Gopło, Skulska Wieś, and Skulskie). The lakes are located in central Poland near the city of Konin. The largest distance between any two lakes is less than 30 km (Fig. 1a). Heated lakes receive water from two power plants, Pątnów and Konin, operating since 1958 and 1970, respectively. Among the heated lakes, three (Gosławskie, Licheńskie, and Pątnowskie) are shallow and polymictic (Licheńskie becomes partially stratified within a very small radius from the deepest point), while the other two (Mikorzyńskie and Ślesińskie) are deep and stratified (*see* Supporting Information Table S1; Fig. S2). Lake Ślesińskie is heated only occasionally, on the hottest days, when the cooling capacity of the other four constantly heated lakes is insufficient for the power plants. A detailed description of the heated lake system can be found in previous studies (Socha and Hutorowicz 2009; Stawecki et al. 2013; Dziuba et al. 2020). Among the control lakes, two (Gopło and Skulskie) are shallow and polymictic, and two are deep and stratified (Budzisławskie, Skulska Wieś; Supporting Information Table S1; Fig. S2). The lakes are inhabited by the *Daphnia longispina* species complex, including *Daphnia*

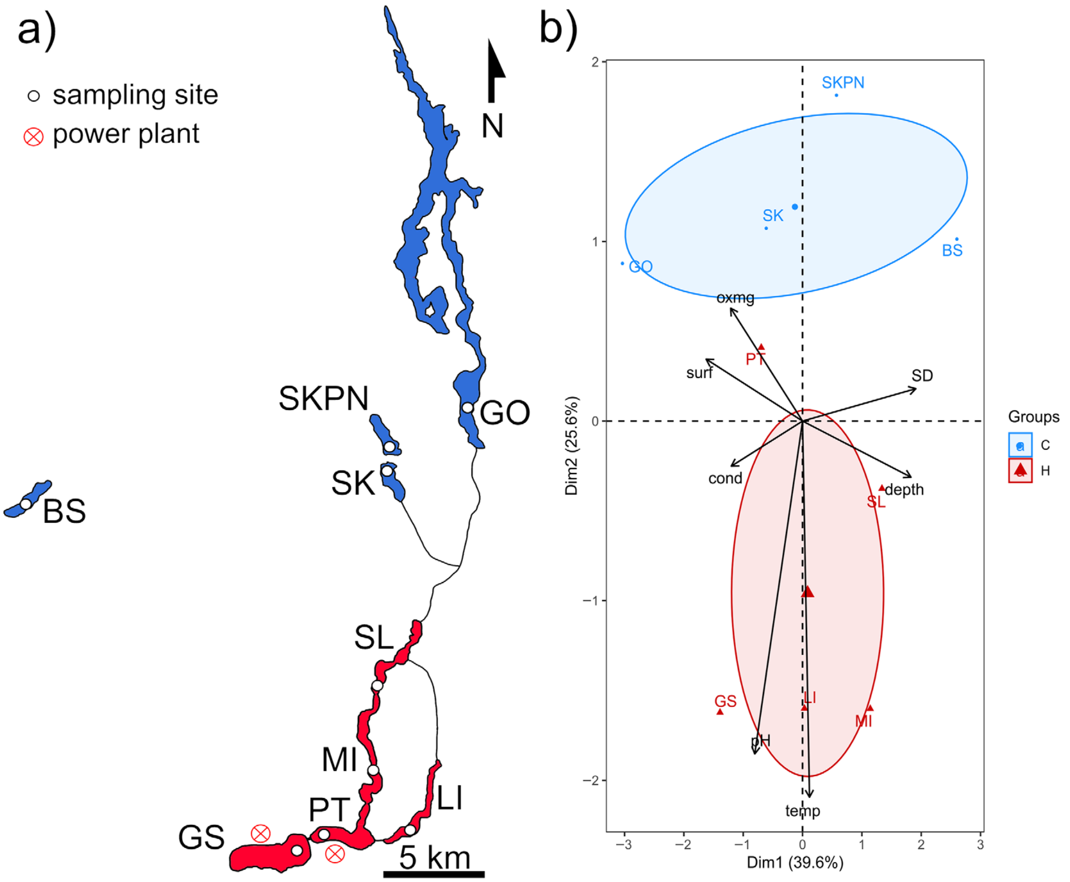

Fig. 1. (**a**) Map of the system (geographical coordinates: 52.4°N; 18.3°E). Heated lakes Pątnowskie (PT), Gosławskie (GS), Licheńskie (LI), Ślesińskie (SL), and Mikorzyńskie (MI) are indicated with red and control lakes Gopło (GO), Skulskie (SK), Skulska Wieś (SKPN), and Budzisławskie (BS) are indicated with blue. (**b**) PCA of lake distribution with regard to environmental descriptors: maximum depth (depth), surface area (surf), electrical conductivity (cond), oxygen concentration (oxmg), pH, surface temperature (temp), and Secchi disc visibility (SD). Red and blue inertia ellipses group heated and control lakes, respectively.

cucullata, *Daphnia galeata*, *Daphnia longipsina*, and their interspecific hybrids (Dziuba et al. 2020).

Daphnia communities were sampled for parasite screening during the autumn season of 5 consecutive years: November 2012, October 2013, and October and November in the years 2014–2016 (control lake Budzisławskie was not sampled in 2013; sampling of control lake Skulska Wieś began in November 2014) (data provided in Supporting Information Table S2). In addition, to rule out potential seasonal differences in disease emergence between types of lakes, monthly sampling was performed in the periods March 2014–August 2014 and October 2014–February 2015 (heated lake Gosławskie was not sampled in May and July 2014; Supporting Information Table S3). Samples of *Daphnia* communities were collected by vertical towing of a 100-μm plankton net through the deepest part of each lake (in the case of lake Gopło, samples were collected from the deepest accessible point). Samples were preserved in ethanol at a final concentration of ca. 70%. In addition, data on the physicochemical parameters of the water column (i.e., temperature, conductivity, pH, total dissolved salts concentration, oxygen concentration, and oxygen saturation) were collected (except for lake Licheńskie in November 2012) with 1 m resolution. The lakes that had thermocline regularly formed during the summer were qualified as stratified, with exception of lake Licheńskie (this lake is stratified only at the deepest spot and overwhelming part of the lake does not undergo stratification; thus, qualifying it as stratified would be misleading; the ecological processes occurring in this lake are typical for a non-stratified lake). Water transparency was measured with a Secchi disc at each sampling station (Secchi depth [SD] corresponds with phytoplankton concentrations and can be used as a proxy for trophic state; Carlson 1977).

Parasite screening

From each sample, 100 randomly selected adult female individuals belonging to the *D. longispina* species complex were inspected using a stereomicroscope at ×250 magnification for presence of *Caullerya*. Infection by *Caullerya* is visible without host dissection, appearing as clusters of large oval spores in the transparent gut of *Daphnia* (Lohr et al. 2010). Presence of other endoparasites (visible without host dissection, i.e., excluding some gut microsporidia) of *Daphnia* was also recorded. The prevalence of each parasite was estimated as a percentage of infected individuals.

Infection experiment

The experiment was performed using *D. cucullata*, the only species consistently found in all of the investigated lakes (Dziuba et al. 2020). In the *Daphnia* community samples in which *Caullerya* was present, this species was always infected (data not shown). Several clones of *D. cucullata* were isolated from two heated (Licheńskie and Pątnowskie) and two control lakes (Skulskie and Gopło) in August–September 2019 and maintained for at least 3 months in laboratory conditions prior to the experiment. These were kept in filtered lake water (collected from lake Kierskie, near Poznań, Poland) mixed with Aachener Daphnien Medium (ADKlüttgen et al. 1994) in a 6 : 1 ratio, with conductivity adjusted to ca. 650 μS cm^{-1}. Cultures were maintained at 20°C, 12:12 h day/night cycle, and fed ad libitum with *Chlorella vulgaris* thrice weekly. Two clones from each lake were used in the experiment. Their cultures were duplicated and split between 16°C and 20°C incubators. Both temperatures fall within the range of successful laboratory infections by *Caullerya* (Schoebel et al. 2011); the 4°C disparity corresponds to the temperature difference between the warmest of the heated and control lakes (*see* supporting information fig. S1 in Dziuba et al. 2021) and to climate change predictions for the year 2100 (Pörtner et al. 2019). When preparing the 16°C treatment, the temperature was ramped down from 20°C to 16°C over 6 d, providing a gradual 0.66°C d^{-1} reduction. *Daphnia* were kept in full darkness to prevent excessive growth of *Ch. vulgaris*. The experiment was started 2 weeks after initiating acclimation to experimental temperatures.

For each clone and at each temperature, 15 experimental glass vials were filled with 5 mL of medium (identical to that used for stock cultures) and 2 randomly selected *Daphnia* individuals were placed in each vial. Due to difficulties in rearing this very small and generally sensitive *Daphnia* species, including particularly high juvenile mortality, experimental individuals were picked from non-age-synchronized cohorts. *Daphnia* were fed every second day, while offspring and/or dead individuals were removed daily. After 7 d (i.e., just before parasite inoculation) excess individuals were removed, leaving one (random) adult *Daphnia* in each experimental vial. The overall experiment included: 2 groups of lakes (heated vs. control) × 2 lakes per group × 2 clones × 2 temperatures × 15 replicates = 240 experimental units.

Parasite spores were isolated from fresh zooplankton samples collected from the control lake Skulska Wieś during a *Caullerya* outbreak in winter 2019/2020. Samples were processed under a stereomicroscope, and *D. cucullata* visibly infected with *Caullerya* were isolated with tweezers and placed in 1.5-mL tubes filled with 0.5 mL of culturing medium (20 individuals per tube). The contents of the tube were then ground with a pestle to obtain a solution of *Caullerya* spores (following protocols established in Schoebel et al. 2011; Tellenbach et al. 2016). Solutions from several tubes were pooled together and vortexed. The resulting spore cocktail was then distributed equally among all experimental *Daphnia*. This inoculation procedure was performed twice (on days 0 and 1 of the experiment, using spores extracted from 240 to 300 infected *Daphnia*, respectively), resulting in a total spore dose of ~ 2.25 infected *Daphnia* per recipient *Daphnia*.

Daphnia were inspected daily for reproduction and mortality and fed ad libitum every second day throughout the experiment. Each individual that died after day 4 of the experiment was inspected under a stereomicroscope for symptoms of parasite infection; detection of earlier infection symptoms is very unlikely (Lohr et al. 2010). The experiment was concluded after 15 d (which is sufficient time for the parasite to develop; Lohr et al. 2010), and all remaining *Daphnia* were inspected for parasite infection.

Statistical analyses

Characteristics of heated and control lakes

Heated and control lakes were compared in terms of their morphometric and environmental descriptors. The physicochemical data collected each October (when *Caullerya* epidemics usually break out; Wolinska et al. 2011) were averaged from 1 m resolution measurements across the water column; in the case of temperature, surface measurements (at 1 m depth) were used instead. Means of physicochemical parameters and values of SD collected over 2013–2016 were further averaged, to provide one value per lake for analysis (Supporting Information Table S1). From pairs of descriptors that correlate (e.g., total dissolved salts concentration correlates with water conductivity, oxygen saturation correlates with oxygen concentration), one (the former) of each pair was removed, leaving only the parameters presented in Supporting Information Table S1. To test if lake descriptors had any relationship with lake type (heated vs. control), a principal component analysis (PCA) was performed. PCA was carried out with and without temperature as a descriptor. The former aimed to assess the contribution of thermal conditions to the grouping between heated and control lakes. The latter was used to investigate whether any additional factor drives divergence between these two groups of lakes.

Distribution of parasites among heated and control lakes

Prevalence of *Caullerya* in *Daphnia* from field samples was coded as presence/absence of the parasite in each individual, and the data analyzed with a generalized linear mixed effects regression model using a binomial distribution (with logit link function). Lake type (heated vs. control) and presence/absence of thermal stratification (which is also directly related to lake depth; *see* Supporting Information Table S1) were used as fixed effects, and lake and year of sampling as random effects. In cases when samples were taken in October and November, the higher parasite prevalence was always used for analysis. The model fitting was followed by type III analysis of deviance.

Infection experiment

Each experimental *Daphnia* was coded as infected or not infected. Parasite prevalence was analyzed in relation to lake type (heated vs. control) and treatment temperature (16°C vs. 20°C) using a generalized linear model, binomial data distribution, and logit link function. Random effects of lake and clone were removed from the model due to overfitting. The interaction term was removed due to lack of significance and its removal improved the Akaike Information Criterion score of the model. The model fitting was followed by type II analysis of deviance. All analyses were performed in R version 3.5 (R Core Team 2018).

Results

Characteristics of heated and control lakes

A comparison of distance between lake type centroids in the PCA of lake morphometry and physicochemical parameters excluding water temperature indicates the similarity of the heated and control lakes (Supporting Information Fig. S1a). When water temperature was included in the PCA, the heated lakes diverged from the control lakes (Fig. 1b; Supporting Information Fig. S1b), indicating that water temperature is the main factor (among the measured parameters) differentiating the heated and control lakes.

Distribution of parasites among heated and control lakes

In the lakes investigated, three types of *Daphnia* parasite were observed: the ichthyosporean *Ca. mesnili*, an oomycete parasite infecting the brood pouch (Tellenbach et al. 2007; Wolinska et al. 2008), and an oomycete parasite infecting the head part (oomycete parasites of *Daphnia* belong to the families Saprolegniaceae and Pythiaceae; Wolinska et al. 2009). The oomycete parasite infecting the brood pouch occurred in one control lake (Skulskie) and three heated lakes (Gosławskie, Licheńskie and Ślesińskie), although in the last two lakes it was found on only one sampling occasion and reached only 1% prevalence. The head infecting oomycete parasite was detected in one control (Skulskie) and one heated lake (Ślesińskie), on only one sampling occasion each, and in lake Ślesińskie it had only 1% prevalence. Because of low prevalence, oomycete-parasite data were not further analyzed.

Caullerya was detected in three of five heated lakes (Mikorzyńskie, Pątnowskie, and Ślesińskie) and in all four control lakes, mostly in autumn samples (with few exceptions: in July in lakes Mikorzyńskie [prevalence: 7%], Ślesińskie [4%], and Skulskie [9%; Supporting Information Table S2]), with a maximum prevalence of 33% (control lake Skulskie, October 2014). Across the three heated lakes in which *Caullerya* was present, the parasite was detected in either one or two out of five consecutive autumns (Fig. 2). In three control lakes (Gopło, Skulskie, Skulska Wieś), *Caullerya* was present every autumn or every autumn except one (in control lake Budzisławskie, *Caullerya* was detected during only one autumn; Fig. 2). Overall, autumn epidemics of *Caullerya* occurred more frequently in control than in heated lakes (lake type $\chi^2_{(1,\ N=4200)} = 17.58$, $p < 0.001$). In control lakes, the parasite prevalence was similar for stratified (deep) and non-stratified (shallow) lakes, whereas in heated lakes *Caullerya* was almost absent in non-stratified lakes (lake type × stratification interaction $\chi^2_{(1,\ N=4200)} = 9.78$, $p = 0.002$, Fig. 3). The adjusted determination index for the model was $r^2 = 0.10$.

Infection experiment

Susceptibility of *D. cucullata* clones from heated and control lakes to infection by *Caullerya* was compared under laboratory conditions at two temperatures: 16°C and 20°C. First symptoms of infection were visible 7 d after parasite inoculation. *Daphnia* that died before this day (the high sensitivity of this species typically results in some background mortality) were excluded from the analysis. *Daphnia* from control lakes were more susceptible to the parasite than those from heated lakes ($\chi^2_{(1,\ N=4200)} = 4.66$, $p = 0.031$; Fig. 4). The experimental temperature did not affect the number of infected *Daphnia* ($\chi^2_{(1,\ N=4200)} = 1.80$, $p = 0.179$). Overall, the prevalence of *Caullerya* was rather low across treatments (the maximum was 22%).

Discussion

Thermal regime is known to affect host–parasite interactions (Mitchell et al. 2005; Hall et al. 2006; Paull et al. 2012). By investigating patterns of infection in host *Daphnia* populations living under different thermal regimes, we aimed to determine whether temperature increase can amplify parasite prevalence. Contrary to the “warmer hence sicker world” scenario, the warmer environment (i.e., heated lakes) coincided with lower parasite prevalence. Although variables other than temperature are known to additionally affect both *Daphnia* and *Caullerya* performance (Schoebel et al. 2010; Tellenbach et al. 2016), it seems that thermal regime—the primary factor distinguishing heated from control lakes—accounts for the discrepancy in the prevalence of the parasite *Caullerya* in the studied lakes. Although the parasite was prevalent in all the control lakes, it was found in only three of the five heated lakes; in heated lakes Mikorzyńskie and Pątnowskie it was detected in one autumn season only and in heated lake Pątnowskie it occurred at a prevalence of only 1%. *Caullerya* is probably transferred from control lakes to heated lakes Mikorzyńskie and Ślesińskie via watercourse connections. Specifically, lake Ślesińskie is connected by a channel to control lakes Gopło and Skulskie on one side and Mikorzyńskie on the other side (Fig. 1a), which may enable migration of both

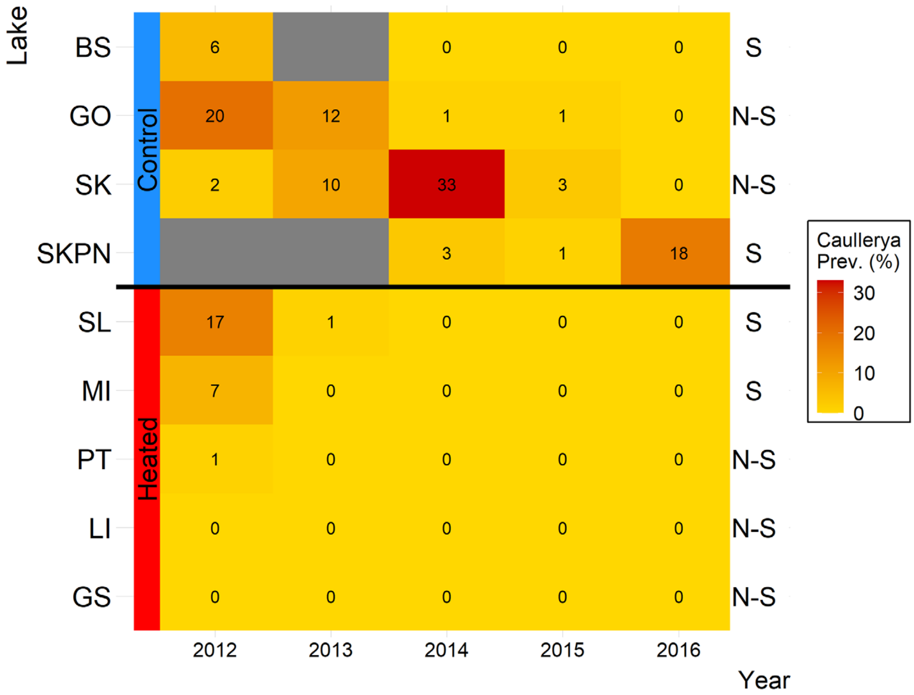

Fig. 2. Heat map of *Caullerya* prevalence in *Daphnia* communities in autumn samples from control lakes Budzisławskie (BS), Gopło (GO), Skulskie (SK) and Skulska Wieś (SKPN), and heated lakes Ślesińskie (SL), Mikorzyńskie (MI), Pątnowskie (PT), Licheńskie (LI), and Gosławskie (GS). Labels S and N-S on the right side of the figure indicate which lake is stratified or non-stratified, respectively. Gray fields indicate lack of data (lakes were not sampled).

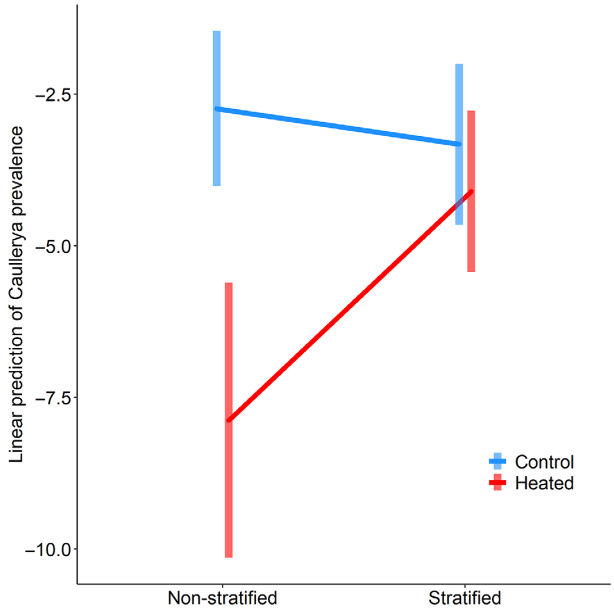

Fig. 3. Post hoc comparison of *Caullerya* prevalence in *Daphnia* communities in heated and control lakes with separation into stratified and non-stratified lakes. Error bars indicate 95% confidence intervals.

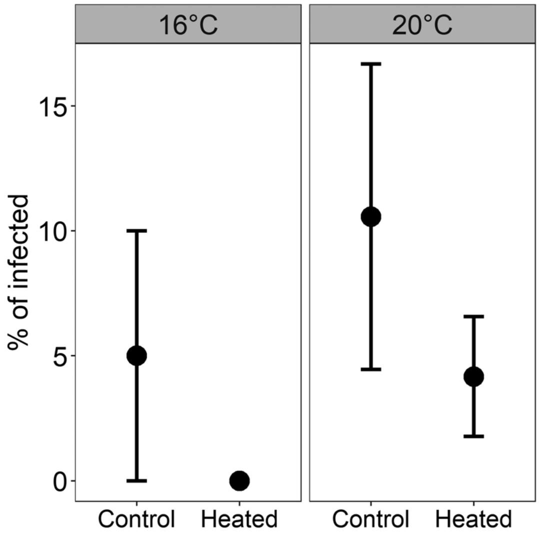

Fig. 4. Comparison of *Caullerya* infection prevalence in experimental *Daphnia* between the two exposure temperatures (16°C and 20°C) and two origins of experimental *Daphnia* (control and heated lakes). Values are calculated as means across four *Daphnia* clones tested within respective treatments. Error bars indicate standard error.

Daphnia and their parasites between heated and control lakes. Due to their larger depth relative to the other, shallower heated lakes, both Mikorzyńskie and Ślesińskie offer a thermal refuge for sensitive organisms. The spatial location (between shallow heated lakes and control lakes) and thermal regime (stratification, i.e., availability of deep cold-water refuge and, in the case of lake Ślesińskie, also less intensive heating) of lakes Mikorzyńskie and Ślesińskie confer their transitional character between lakes heated throughout the entire water column and control lakes (Dziuba et al. 2020). Our data suggest that, as such, these deep, heated lakes can occasionally facilitate the spread of *Caullerya*. By contrast, the parasite was unable to spread through shallow heated lakes Gosławskie, Licheńskie, and Pątnowskie (except year 2012 in Pątnowskie), which are warmer than control lakes across the entire water column (Supporting Information Fig. S2; *see* also fig. S1 in Dziuba et al. 2021 for a comparison of summer temperature profiles). The outbreak of disease only in the two heated lakes that offer thermal shelter further corroborates the conclusion that thermal regime shapes the *Daphnia*–*Caullerya* interaction and that temperature increase might have created conditions detrimental to the latter.

Although the parasite was occasionally able to infect the host in three heated lakes, it could not spread successfully through the entire heated lake system. Our laboratory experiment confirmed that *Caullerya* spores do not lose their infectiousness even at 20°C, conditions much warmer than those during the peak of epidemic. Hence we reject the explanation that the higher temperature of heated lakes during the epidemic season is driving this pattern. We considered the idea that due to temperature elevation, the epidemics in heated lakes might start later (based on temperatures in control lakes during peak epidemics we would predict that epidemics in heated lakes would peak a month later). However, the analysis of samples taken monthly from October 2014 through February 2015 indicates no delay in disease outbreak in heated lakes that we would potentially miss, by analyzing autumn samples only (Supporting Information Table S3). Both types of lakes are inhabited by species from *Daphnia longispina* complex, and differ in relative frequencies of some of the species (Dziuba et al. 2020), but it seems unlikely that the difference in infectiousness of *Caullerya* between *Daphnia* communities in heated lakes and control lakes stems from the interspecific differences in host's susceptibility to the parasite. First, all the species of *Daphnia longispina* complex, that are present in both heated and control lakes, have been shown to be susceptible to *Caullerya*—outside this heated and control lakes system (Wolinska et al. 2007). This indicates lack of strong taxonomy-related differences in resistance. Second, our morphological observations indicate that *D. cucullata* (present in all investigated lakes, frequently in high ratios, Dziuba et al. 2020) and/or its hybrids were predominantly the host for *Caullerya* in both heated and control lakes. Nevertheless, in the laboratory experiment we used only *D. cucullata* clones from heated and control lakes, considering the possibility that *Caullerya* is locally adapted to a specific set of host clones (Greischar and Koskella 2007).

The experiment was performed to ascertain whether *Caullerya* is less infectious in warmer conditions or if *Daphnia* clones originating from heated lakes are more resistant, but also to separate the factors of temperature and origin from all the other potentially contributing factors. The experiment showed that *D. cucullata* clones originating from heated lakes were more resistant than conspecifics from non-heated lakes, regardless of rearing temperature. Also, the applied temperatures did not harm the spores, indicating that spores of *Caullerya* remain infectious in thermal conditions present during the disease outbreak season in both heated and control lakes. This implies that the distribution of *Caullerya* among heated and control lakes is driven by the interplay of local adaptation of the parasite and other contributing factors, most likely indirect effects of temperature increase, constraining the parasite in heated lakes.

The parasite spores were isolated from control lake Skulska Wieś, which is in close proximity to control lakes from which experimental *Daphnia* were isolated (lakes Gopło and Skulskie), whereas the heated lakes from which experimental *Daphnia* were collected (lakes Licheńskie and Pątnowskie) are more distant. The parasite's higher propensity to infect sympatric hosts suggests that it is locally adapted (Greischar and Koskella 2007). Local adaptation occurs when the host–parasite interaction is genotype-specific (Gandon 2002), and some degree of specificity seems present in the *Daphnia*–*Caullerya* interaction (Wolinska et al. 2006; Turko et al. 2018). Specialization in overcoming defense mechanisms of local hosts gives locally adapted parasites an advantage in infecting sympatric host populations with which it coevolved, at the cost of reducing their ability to infect allopatric hosts. There is no evidence for genetic divergence between host (*D. cucullata*) populations from heated and control lakes measured at neutral loci (Dziuba et al. 2020). Nonetheless, immune defense-related genes—usually the fastest evolving genes (McTaggart et al. 2012)—could have diverged as a result of selection pressure from *Caullerya* infection present in control lakes but not in heated lakes. Lack of a coevolutionary history probably impaired the parasite's ability to successfully invade allopatric hosts from heated lakes. An ultimate confirmation of parasite local adaptation could be attained by performing experimental infections with *Caullerya* spores extracted from heated lakes. It was not possible to perform such experiment as at the time when the experiment was performed the parasite was not detected in those lakes, making it impossible to obtain the spores.

Our experiment showed that the temperature difference between heated and control lakes during the time of epidemics is unlikely to be the cause of lack of *Caullerya* in heated lakes. Mass *Caullerya* infections usually occur in autumn and winter (Wolinska et al. 2011; Turko et al. 2018), when ambient temperatures are low, and (based on the results of the experiment) the ca. 3–4°C temperature elevation does not seem to directly drive parasite distribution and infectivity in the investigated lakes. It is thus plausible that conditions lethal to the parasite (i.e., excess temperature) occur outside the typical disease outbreak season. Elevated summer temperature might be harmful to the transmission stages of the parasite (assuming that the spores in fact come into contact with such high temperatures) and hamper its dispersion and establishment in heated lakes, even though *Caullerya* epidemics do not occur in the summer. The contact of parasite spores with extreme temperatures could be facilitated by temperature elevation-driven changes in crucial hydrological features of the lakes (e.g., mixing regime). Below we describe how these changes might expose *Caullerya* to potentially harmful high temperatures and prevent its dispersion to *Daphnia* populations in heated lakes.

What happens to *Caullerya* after the disease peak is uncertain. It might be that parasite spores sink to the bottom sediments of the lake during winter stagnation and become active again after resuspension during the next mixing periods (as seen with many other *Daphnia* parasites; Ebert 2005; Decaestecker et al. 2004). Warm—and thus suboptimal—summer conditions might potentially be evaded by at least some fraction of *Caullerya* spores buried in sediments. Some fraction of spores might be resuspended by spring turnover, but in case of lowland Central-European lakes *Caullerya* outbreaks seem to be synchronized with fall rather than spring mixing (Wolinska et al. 2011, this study). In the case of heated lakes, and particularly the shallow ones, ice cover occurs very rarely (Socha and Hutorowicz 2009; M. K. Dziuba and S. Cerbin pers. observ.), and without the ice cover there is no winter stagnation. Such conditions facilitate constant mixing from autumn until summer stratification the following year, due to which parasite spores would have a smaller chance of becoming buried in lake sediments. Spores might instead remain in the water column where they would be exposed to potentially detrimental sunlight (Rogalski and Duffy 2020) and high summer temperatures. In heated lakes, mean summer epilimnion temperatures oscillate around 24°C (Dziuba et al. 2021; Supporting Information Fig. S1), but the annual maximum quite often reaches about 28–30°C (M. K. Dziuba and S. Cerbin pers. observ.). If the extremely high summer temperature is indeed harmful to the spores, then even if *Caullerya* invades heated lakes, its spores might lose their infectivity every summer, after being exposed to warmer conditions. Such periodic removal of spores would prevent *Caullerya* establishment in heated lakes. That would in turn drive local adaptation of the parasite to *Daphnia* clones from control lakes (as detected in our experiment) and both would lead to differential distribution of *Caullerya* among heated and control lakes (observed in the field samples). Our evidence that the temperature of the heated lakes is deadly to the spores is only circumstantial: first, that *Caullerya* seems to be thriving in lakes late in the season when the temperatures are lower, and second, epidemics are not observed after the spore resuspensions in spring (Wolinska et al. 2011). Performing a similar experiment but with broader range of temperatures, especially spanning over 20°C, would help to determine what is the thermal range for *Caullerya* spore survival/infectivity, and verify whether the summer temperatures can be detrimental to the parasite. Such experiment should use field collected spores; hence our ability to run it was limited by the timing of disease outbreak in the studied lakes.

The exclusion of some parasites and consequent decrease in parasite-mediated selection pressure, as experienced in heated lakes, might have far-reaching consequences for *Daphnia* populations. Parasites promote sexual reproduction in host populations (Jaenike 1978; Jokela et al. 2009). In the case of cyclical parthenogens such as *Daphnia*, lack of parasites might result in more frequent clonal reproduction and reduced genetic recombination. *Daphnia* seem to curtail the production of sexual eggs under temperature elevation (Tsugeki et al. 2009; Zeis et al. 2010; Dziuba et al. 2020), and further reduction in the frequency of sexual reproduction might lead to low genetic diversity and inbreeding depression, which leaves populations more exposed to environmental threats and increases the risk of extinction (Haag et al. 2002). Parasites in general can have crucial functions in food webs, for example, by controlling host populations and taking a role in energy flow (Lafferty et al. 2006, 2008). Since many zooplankton-infecting parasites diapause in sediments (Green 1974; Decaestecker et al. 2004; Ebert 2005), the alterations in seasonal turnover and in cyclical spore resuspension (proposed as potential explanation of the infection pattern identified in our study), might be applicable to other parasite species.

The favorable impact of global temperature increase on the performance of parasites, in line with the "warmer hence sicker world" hypothesis, is certainly true for some host–parasite systems (Brooks and Hoberg 2007; Marcogliese 2008; Shocket et al. 2019). However, the impact of temperature increase on host–parasite dynamics might be asymmetrical (Kirk et al. 2018), being more costly to the parasite than to the host (Berger et al. 2004; Raffel et al. 2010; Gehman et al. 2018), and also entail indirect effects, for example, altered hydrology or winter conditions (Marcogliese 2001). Incorporating direct and indirect effects of warming will increase the accuracy of predictions of climate change impact on organisms' interactions. This is difficult to achieve, as it would require simulation of warming conditions on a whole ecosystem scale. Therefore, heated ecosystems like the lakes used in this study can be very convenient research models for addressing climate change related questions. The heated lakes studied here have been receiving warm water from power plants for 60 yr, resulting in elevated temperatures within realistic global warming scenarios. They offer a unique opportunity to observe modifications of host–parasite interactions in a warming world. Our study showed that in heated lakes, host *Daphnia* is less infected by its parasite *Ca. mesnili*. We conclude that the temperature elevation prevents maintenance of the parasite in heated lakes and coevolution with the host in control lakes further inhibits re-establishment of *Caullerya* from control to heated lakes. Disappearance of a parasite from the ecosystem might induce a disruption of its functioning (Buck 2019; Carlson et al. 2020). Exploring how parasites respond to elevated temperatures via studies performed in natural, large-scale settings, is essential for predicting disease spread in a warmer world.

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Conflict of interest statement

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