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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Some like it hotter: trematode transmission under changing temperature conditions

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Abstract
Climate change-related increases in temperature will influence the interactions between organisms, including the infection dynamics of parasites in ecosystems. The distribution and transmission of parasites are expected to increase with warmer temperature, but to what extent this will affect closely related parasite taxa living in sympatry is currently impossible to predict, due to our extremely limited understanding of the interspecific variation in transmission potential among parasite species in changing ecosystems. Here, we analyse the transmission patterns of four trematode species from the New Zealand mudsnail *Potamopyrgus antipodarum* with different life cycles and transmission strategies under two temperature scenarios, simulating current and future warmer temperatures. In a comparative experimental study, we investigated the effects of temperature on the productivity, movement and survival of the parasites' transmission stages (cercariae) to quantify the net effect of temperature on their overall transmission potential. Our results show that increases in temperature positively affect cercarial transmission dynamics, yet these impacts varied considerably between the cercariae of different trematode species, depending on their host-searching behaviour. These different species-specific transmission abilities as well as the varying individual patterns of productivity, activity and longevity are likely to have far-reaching implications for disease dynamics in changing ecosystems, since increases in temperature can shift parasite community structure. Due to the parasites' capacity to regulate the functioning of whole ecological communities and their potential impact as disease agents, understanding these species-specific parasite transmission traits remains a fundamental requirement to predict parasite dynamics under changing environmental conditions.

Keywords Parasite · Diseases ecology · Global climate change · Aquatic ecosystems

Introduction

Global warming poses serious threats for ecosystems on all continents and across oceans, and its impacts constitute a central challenge for current and future generations (IPCC 2014). Understanding and potentially predicting these changes remain major scientific tasks. Across all ecological systems, temperature significantly influences the strength and outcome of interactions between and among species (Araújo and Luoto 2007; Gilman et al. 2010; Traill et al. 2010; Woodward et al. 2010). The interactions between parasites and pathogens and their free-living host organisms have been shown to be particularly sensitive to climate change and related anthropogenic impacts, such as habitat alterations or biological invasions, with potential wide-reaching effects on whole ecosystems (Harvell et al. 2002; Jones et al. 2008; Altizer et al. 2013; Pecl et al. 2017). Under changing climate conditions, the relative abundance of different parasite species is expected to change, as would their relative impacts on host populations and entire communities. Assessing the interactions and their potential changes and impacts requires a thorough understanding of the ecology and transmission dynamics of parasitic organisms.

From a parasite's point of view, hosts represent habitable and resource-rich 'islands' within an energy-low and often hostile environment (Kuris et al. 1980). Whilst being on these islands, that is on or within a host, is not without

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risks (e.g. the host's immune defences need to be evaded), it is the gap between these islands that presents the major barrier parasites need to overcome. In short, transmission between hosts is a risky undertaking and a major determinant of the parasites' fitness (Parker et al. 2003). The success of these transmission events therefore shapes and structures parasite communities in ecosystems and determines disease dynamics. Changing climatic factors can differentially impact the transmission success of co-occurring parasite species (Koprivnikar and Poulin 2009). Therefore, assessing the influence of temperature on the transmission of different parasites is a key step toward predicting how local parasite communities will respond to a changing climate.

One approach to the risky transmission problem of parasites is the ability to multiply asexually in an intermediate host and produce many genetically identical dispersal stages to increase the odds that some individuals will reach the next target host (Poulin 2011). This strategy is particularly suitable for transmission in aquatic systems where free-living stages can disperse and seek out suitable hosts. Asexual multiplication in an intermediate host is a characteristic of the diverse group of digenean trematodes, in which most life cycles are at least partially aquatic (Cribb et al. 2003). With a cosmopolitan distribution and about 25,000 species, digenean trematodes constitute the most common metazoan pathogens in aquatic ecosystems, including species of medical or veterinary relevance, such as *Schistosoma* spp. or *Fasciola* spp. (Esch et al. 2002; Morley et al. 2006). During their life cycle, trematodes utilize a wide variety of vertebrate definitive hosts, including fish, birds or mammals, but share a unifying character in requiring molluscs (usually snails) as first intermediate hosts. In the snail, free-living dispersal stages of the parasite, the cercariae, are produced asexually in large numbers. Cercariae then leave the snail to seek out and infect their next vertebrate or invertebrate host.

Depending on the parasites' environment, life strategies and target host, trematodes have evolved a huge diversity in cercarial size, morphology and behaviour (Esch et al. 2002; Koehler et al. 2012; Morley 2012). Features such as size, morphology or numbers of transmission stages produced result from trade-offs among a number of factors, ranging from resource availability (i.e. snail size) and second intermediate host identity (abundance, mobility, etc.) to environmental factors (Koehler et al. 2012). Cercariae are typically short-lived (< 24 h) and their functional life span, i.e. the time during which they are infective, is often even shorter (Toledo et al. 1999; Karvonen et al. 2003). Accordingly, the timing of emergence from the snail host is often synchronized with the target host's main period of activity (host time) and the cercariae move to positions in the water column where host encounters are most likely (host space) to maximize the chances of transmission (Combes et al. 1994; Morley 2012; Thieltges and Rick 2006). In the water, cercariae then display distinctive and species-specific movement patterns in their search for their respective target hosts (Selbach and Poulin 2018), and can use visual, tactile or chemical cues to find a suitable host organism (Haas 2003).

Once cercariae have left their snail host, they are subject to a wide range of environmental conditions that affect their survival, dispersal and transmission to the next host organism. These ambient factors include both biotic and abiotic components that can severely impact the distribution and abundance of parasites in ecosystems (reviewed in Pietrock and Marcogliese 2003; Thieltges et al. 2008a). For example, changes in ocean acidification, salinity and temperature show complex interactive effects on the survival of trematode cercariae in marine ecosystems (Koprivnikar et al. 2010; Franzova et al. 2019), while eutrophication of water bodies can promote transmission and infection levels of these parasites (Johnson and Chase 2004; Johnson et al. 2007). On the other hand, non-host organisms that act as predators, dead-end hosts or physical barriers to the fragile cercarial stages can significantly reduce parasite transmission dynamics in aquatic systems (Mouritsen and Poulin 2003; Thieltges et al. 2008b; Johnson et al. 2010; Welsh et al. 2017; Vielma et al. 2019; Selbach et al. 2019).

With regard to the potential impacts of climate change and global warming on disease ecology, several experimental studies have examined the impacts of temperature on the transmission abilities of trematode cercariae, sometimes with unexpected or contrasting results (see Marcogliese 2016). While cercarial productivity and output from the snail host have been shown to be strongly temperature dependent and typically increase with higher water temperatures, at least up to a point (Poulin 2006; Studer and Poulin 2013), other studies have found contrasting results with varying responses of trematode cercariae to temperature increases (Koprivnikar and Poulin 2009; Morley and Lewis 2013). Moreover, other steps in the transmission of cercariae are impacted by changing temperatures, such as activity, survival time or infectivity in the target hosts, most likely because the limited energy reserves of the non-feeding cercariae will be depleted at higher rates under warmer temperatures (Marcogliese 2001; Thieltges and Rick 2006; Studer et al. 2010).

Altogether, climate change and global warming are expected to significantly alter transmission dynamics and likely increase infection levels of trematodes in most ecosystems (Marcogliese 2001; Poulin 2006; Poulin and Mouritsen 2006). However, to what extent this will affect different trematode species is hard to predict, since we still have an extremely limited understanding of the interspecific variation in dispersal potential among parasite species. Because trematode cercariae show a wide variety of morphological and behavioural differences, extrapolating from studies focusing on single parasite species can lead to erroneous predictions and generalizations regarding the impacts of climate change on parasite transmission (Marcogliese 2016). If individual trematode species react differently, then under changed climatic conditions the relative abundance of these parasite species may be changed, as would their relative impacts on host populations and the entire community.

To close this knowledge gap, the present study focuses on a single trematode community, sharing the same snail intermediate host, and investigates how it responds to changing temperatures. We disentangle the individual components of cercarial transmission of four trematode species under two temperature scenarios to (i) quantify how temperature affects the output, activity and survival of trematode cercariae in their search for a suitable target host, (ii) to test whether these cascading effects offset each other or lead to a stronger net effect, and (iii) to test whether different trematode species react differently to temperature changes. Based on known temperature responses of trematodes, we hypothesize that temperature will positively affect cercarial output from the snail host and movement of individual cercariae, but will negatively impact cercarial survival rates. Overall, we expect a positive net effect on the dispersal capabilities of individual trematode cercariae under a higher temperature scenario, but with substantial differences among the four trematode species, based on their distinctive life strategies, host-searching behaviour and morphology.

Materials and methods

Concept and study species

Assessing the full impact of temperature on the cercarial transmission process would ideally entail measuring the actual infection success of the individual parasites in their target host (and ultimately the successful completion of the parasite's whole life cycle, see Marcogliese 2016). However, temperature changes would similarly affect different hosts' susceptibility to parasitism (e.g. via behavioural or immune responses) to varying degrees. To measure the effect of temperature on the active dispersal and transmission abilities of trematode species, we therefore separated the transmission process into three main components that could be assessed individually under different temperature scenarios (Fig. 1). These components were: (i) output, i.e. the number of cercariae emerging during a defined time span; (ii) movement, i.e. the movement of cercariae during a defined time span as an indicator of their activity and ability to actively search out their respective target hosts in the aquatic environment; and (iii) survival, i.e. the time span cercariae remain fully active and potentially infective.

We selected four common trematode species of the New Zealand mudsnail *Potamopyrgus antipodarum* (Gray 1843) that serves as an important first intermediate host to a diverse fauna of trematodes in freshwaters (Hechinger 2012; Lagrue and Poulin 2015): *Coitocaecum parvum* (Opecoelidae), *Maritrema poulini* (Microphallidae), *Apatemon* sp. (Strigeidae) and *Aporocotylid* sp. I (Aporocotylidae). These four species belong to different families and represent contrasting trematode life histories and life cycles with two target host groups, either crustaceans (*C. parvum*, *M. poulini*) or fishes (*Apatemon* sp., *Aporocotylid* sp. I). The cercariae of these four species exhibit different movement and behavioural patterns, reflecting their individual host-searching strategies, based on their respective target hosts' ecology and distribution (Selbach and Poulin 2018). We chose two water temperature scenarios, 16 °C and 20 °C, based on the seasonal range of shallow waterbodies in Otago, New Zealand, where the snails were collected (Hall and Burns 2002). Due to the region's cool summer climate, 16 °C reflects moderate summer water temperatures, whereas 20 °C represents temperature peaks at the upper end of the range that can be expected to be more frequent under future climate changes.

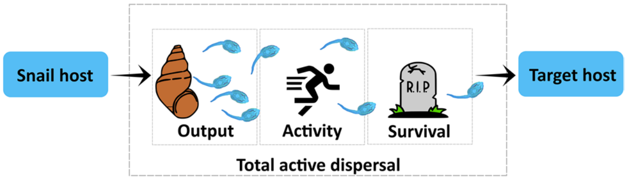

Fig. 1 The individual components of trematode cercarial transmission between snail and target host

Collection of samples

Snails, *Potamopyrgus antipodarum*, were collected from macrophytes, sediment and stones along the shoreline of Lake Waihola (46°01′14S, 170°05′05E) and Tomahawk Lagoon (45°54′S, 170°33′E), New Zealand, using dip nets. Snails were brought back to the laboratory and separated into individual wells of 24-well plates with small amounts of filtered lake water and incubated for 24 h at 20 °C under a light source to induce cercarial shedding and identify patent trematode infections. Cercariae were identified based on morphological features, using the keys of Hechinger (2012) and Presswell et al. (2014). We isolated snails infected with the relevant trematode species (*C. parvum*, *M. poulini*, *Apatemon* sp. and *Aporocotylid* sp. I). Infected snails were grouped according to their trematode species and kept in aquaria with aerated lake water and macrophytes (*Myriophyllum triphyllum* and *Elodea canadensi*) for food at a constant temperature (16 °C) and under a 12 h/12 h light/dark photoperiod until the beginning of the individual experiments. Since each of the following experiments was conducted at two temperatures (16 °C and 20 °C), infected snails were given at least 24 h to acclimatize to the respective temperature before being used in the experiments. Experiments were conducted over several days, with a mixture of the different trematode species used on each day.

Experiment I: cercarial output

The cercarial productivity of each trematode species was assessed by counting cercariae emerging from individual snails over a period of 48 h under constant temperatures and controlled 12 h/12 h light/dark photoperiods. Infected snails were placed in individual well plates containing 2 ml of filtered lake water and incubated in a temperature chamber at 16 °C/20 °C. Photoperiods were set up from 7 am to 7 pm (light) and 7 pm to 7 am (dark). After a 24 h acclimatization period in the well plates under these conditions, the experiment commenced and the number of cercariae emerged from each snail was assessed for 48 h. After emission period intervals at 7 am, 1 pm and 7 pm, snails were transferred to new well plates with fresh water and the number of cercariae in the old well plates was counted under a stereo microscope. At least 16 individual infected snails per trematode species were used to assess the mean cercarial outputs. Each snail was used in both temperature treatments. To avoid confounding effects of the temperature treatment sequence, treatments were alternated, i.e. half of the snails were used in the warm conditions first, followed by the cold treatment, and the other half of the snails were first used in the cold treatment followed by the warm treatment. The data was then grouped together for each temperature treatment. To avoid confounding effects of snail size, infected snails used in the experiment were of similar size (shell length 4–5 mm), with the exception of *C. parvum*-infected snails (shell length 2–3 mm), which are typically smaller, due to parasite-induced alterations in shell shape and length (Lagrue et al. 2007).

Experiment II: cercarial movement

We assessed the movement of cercariae as an indicator of their activity and ability to actively search out their respective target hosts in the aquatic environment. Individual cercarial movement patterns were measured using the video tracking methods described by Selbach and Poulin (2018). To obtain cercariae for the swimming assessment, infected snails (after a 24 h acclimatization period) were placed in a small Petri dish containing 2 ml of filtered lake water and incubated in a temperature chamber at 16 °C/20 °C under constant illumination for 2 h. Since cercarial activity and infectivity decrease with age, all cercariae used in the experiments were of the same ‘age’ (< 2 h). For the experiment, active cercariae were haphazardly selected and individually transferred to a microscope well slide containing a measured volume of filtered lake water at 16 °C/20 °C. The volumes of water chosen for the experiments allowed the cercariae to move horizontally, while the camera could record their movement; vertical movement was restricted in the selected water volumes, ensuring that cercariae remained in focus (see Selbach and Poulin 2018). The well slide containing a single cercaria was then transferred onto the dissecting microscope and left for a 2-min acclimatization period, to allow cercariae to resume normal movement after pipetting. Subsequently, each specimen was filmed and recorded for 5 min under a dissecting microscope (Olympus SZ61) fitted with a top-mounted Olympus DP25 camera. Lighting was provided by a SZX2-ILLT circular light unit to avoid unidirectional illumination and potential effects on cercarial phototaxis. To minimize the effects of changing water temperature during the course of the experiment, each cercaria was only filmed for 5 min. For each trematode species, at least 17 individual cercariae were recorded at 16 °C and 20 °C, resulting in a dataset of at least 85 min of host-searching behaviour per parasite species and temperature scenario. Based on the videos, the individual movement was automatically tracked using EthoVision XT 11.5 (Noldus Information Technologies). The program distinguishes between the tracking subject and background based on grey values and contrast or colour values of the pixels in each video frame (see Noldus et al. 2001). We measured the total distance moved (in mm) by the individual cercariae as an indicator of dispersal activity.

Experiment III: cercarial survival

To obtain cercariae for survival experiments, infected snails (after a 24 h acclimatization period) were placed in a Petri dish containing 2 ml of filtered lake water and incubated in a temperature chamber at 16 °C/20 °C under constant illumination for 2 h. Freshly emitted active cercariae were haphazardly selected and individually transferred to separate wells of 96-well plates containing 100 µl of filtered lake water each. For the larger cercariae of *C. parvum*, 24-well plates with larger wells containing 500 µl of filtered lake water each were used. All cercariae were checked and specimens that appeared damaged or immobile were not used in the experiment and discarded. At least 40 individual cercariae per species and temperature treatment were monitored to assess the survival curves of the trematode larvae. The well plates with cercariae were incubated in temperatures chambers at 16 °C and 20 °C, respectively, under constant illumination (cold light source). Cercarial activity was checked and recorded after 2, 4, 6, 8 and 10 h and cercariae were visually classified as fully active (showing normal activity, without external stimulus), slow (showing limited movement, or only sluggishly respond to a mechanical stimulus with a fine needle), or dead (cercariae broken or showing no response to mechanical stimulus). Only fully active cercariae were considered functionally alive and counted. Since activity of cercariae of *Maritrema novaezealandensis* (a marine species closely related to *M. poulini*) has been shown to typically cease within 12 h post-emergence (Studer et al. 2010), and cercarial infectivity decreases with age (Thieltges and Rick 2006), we concluded the experiment after 10 h to avoid overestimating cercarial longevity beyond their infective phase.

Statistical analyses

Statistical analyses were performed with GraphPad Prism (V. 5) to test for differences between the two temperature treatments among the individual trematode groups. For the cercarial shedding experiment, we compared the numbers of emerged cercariae per snail during the 48 h experiment, using the nonparametric Mann Whitney test, since data was not normally distributed. Data of the swimming behaviour experiment was normally distributed and we used an unpaired t-test to compare the means of the two temperature treatments. In order to compare the survival rates of cercariae under the different temperature treatments, log-rank (Mantel–Cox) tests were performed to test for differences in the temperature-specific survival curves.

Total active cercarial dispersal

To compare the dispersal capabilities of trematode cercariae under the different temperature scenarios, we designed and calculated a composite index of the potential for cercariae to reach new hosts: the total active cercarial dispersal. For this, we first calculated the cumulative hours of cercarial activity based on the mean daily number of larvae emerged per snail under each temperature scenario and the temperature-specific survival rates, i.e. how many cercariae remain active after 2, 4, 6, 8 and 10 h. We then multiplied this number by the mean distance travelled by a single cercaria per hour. The resulting value provides a combined metric to compare the net effects of temperature on the individual dispersal capabilities (output, survival, movement) of trematode cercariae, i.e. the combined distance travelled by all the cercariae produced by a single snail during a day, taking into account the temperature-specific survival curves. Our measurements of cercarial movement (5 min, see Experiment II) do not account for potential changes in activity rate over the cercarial life span and might therefore slightly overestimate the total movement. However, in the survival experiment, we did exclude cercariae that appeared slow or sluggish, thereby partially controlling for this decrease in activity. Since, in the majority of cases (but see Lagrue et al. 2007), all asexually produced cercariae from a single infection are genetically identical clonal stages of the same trematode individual, with the sole function of transmitting the parasite from one host to another, this metric allows to compare the relative differences in transmission ability between the different temperature treatments. Although the transmission success of trematodes depends on their ability to encounter a host in a three-dimensional water column, this linear description of active dispersal can serve as an indicator of the parasites' ability to maintain and control their position in the host space (see Morley 2020).

Results

Cercarial output varied between and within species, but all species showed an increase in cercarial emergence from 16 °C to 20 °C (Table 1; Fig. 2). Since data were not normally distributed, we compared the medians between the temperature treatments, which only showed significant differences for *M. poulini* (Mann Whitney test, $U = 123$, $P = 0.0054$). Maximum output rates per snail 48 h^{-1} ranged from 44 cercariae for *C. parvum* at 16 °C to 637 cercariae at 20 °C for *Aporocotylid* sp. I.

The measurements of total distance moved (mm 5 min^{-1}) revealed varying results for different trematode species (Table 1; Fig. 3). The cercariae of *M. poulini* showed a significant increase in movement between 16 °C and 20 °C ($t = 7.167$, $df = 32$, $P < 0.0001$), whereas the activity levels in *Aporocotylid* sp. I decreased ($t = 2.864$, $df = 32$, $P = 0.0073$). Neither *C. parvum* ($P = 0.7387$) nor *Apatemon* sp. ($P = 0.8644$) showed significant differences between temperature treatments.

Cercariae of all species showed lower survival rates after 10 h at 20 °C compared to 16 °C, though with varying

Table 1 Percent change between mean daily output per snail, survival time, distance moved and the total active cercarial dispersal from 16 °C to 20 °C

Species	Mean daily output/snail (%)	Mean survival time of cercariae (%)	Mean distance moved (%)	Total active cercarial dispersal (m/24 h) (%)
M. poulini	+276	− 42	+41	+205
C. parvum	+39	− 14	+3	+23.4
Aporocotylid sp. I	+73	− 7	− 27	+17.1
Apatemon sp.	+94	− 8	− 1	+76.7

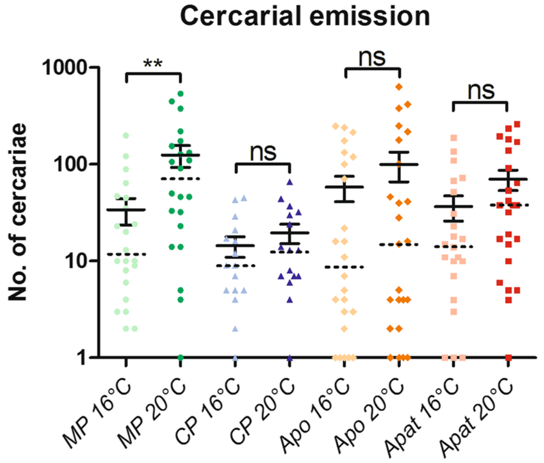

Fig. 2 Number of cercariae emerged from individual snail hosts during a 48 h interval at 16 °C and 20 °C. Data shown on a $\log_{10}+1$ scale. Error bars show mean with SEM; dotted lines show medians. Asterisks above plots denote statistically significant differences between temperature treatments (**$P<0.01$, *ns* not significant; Mann Whitney test). Sample size for each treatment $N \geq 16$. *MP Maritrema poulini*, *CP Coitocaecum parvum*, *Apo Aporocotylid* sp. I, *Apat Apatemon* sp.

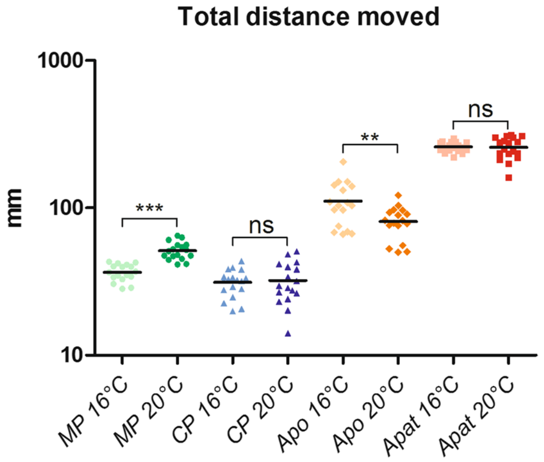

Fig. 3 Total distance moved by individual cercariae during a 5 min interval at 16 °C and 20 °C. The line across the scatterplots indicates the mean. Asterisks above plots denote statistically significant differences between means of temperature treatment groups (**$P<0.01$; ***$P<0.0001$; *ns* not significant; unpaired *t* test). Sample size for each treatment $N \geq 17$. *MP Maritrema poulini*, *CP Coitocaecum parvum*, *Apo Aporocotylid* sp. I, *Apat Apatemon* sp.

survival curves (Fig. 4). The difference was most pronounced in *M. poulini* (Mantel–Cox test; $P<0.0001$), where no larvae remained alive at 20 °C after 10 h, and *Apatemon* sp. ($P=0.0009$). However, the survival curve of the latter species showed an initially slower decrease followed by a sharp decline after 8 h. *Aporocotylid* sp. I showed a statistically significant difference between survival curves (but only marginally, $P=0.0494$), and there were no significant differences in the curves for *C. parvum* ($P=0.2077$), although mortality was higher at 20 °C. Table 1 shows the percent change in mean cercarial survival time based on the individual survival rates.

To compare the dispersal capabilities of trematode cercariae under the different temperature scenarios, we calculated the total active cercarial dispersal, i.e. the combined distance travelled by all the cercariae produced by a single snail during a day, taking into consideration their survival rates. The resulting metric shows that the dispersal capability of all trematode larvae increases under the higher temperature scenario, although to different degrees, ranging from a modest increase by 17% for *Aporocotylid* sp. I to a substantial increase by 206% for *M. poulini* (Table 1; Fig. 5).

Discussion

Climate change-related increases in temperature will influence the strength and outcome of interactions between and among species, including the transmission and infection dynamics of parasitic species (Jones et al. 2008; Gilman et al. 2010; Altizer et al. 2013). In general, transmission rates of parasites are expected to increase with increasing temperatures (Marcogliese 2008), but how differently closely related parasite taxa living in sympatry will react is still impossible to predict. Here, we analysed the transmission potential of four trematode species with different cercarial morphotypes, behaviour and life cycles under two temperature scenarios, simulating current and potential future warmer temperatures.

We hypothesized that temperature would positively affect cercarial output from the snail host and dispersal activity of individual cercariae, but would negatively impact cercarial survival. However, the results from the different experiments presented a more complex picture. Higher temperatures significantly boosted cercarial productivity of one species, while other species showed positive but non-significant upwards trends. More strikingly, cercarial movement revealed highly different species-specific responses to increasing temperature, ranging from strong increases to decreases in movement, or no significant changes. As a result, survival time was most negatively impacted under increased temperature for the parasite species that also exhibited an increased swimming behaviour. Since cercariae are non-feeding transmission stages, greater activity most likely results in a more rapid depletion of their limited energy reserves (McCarthy 1999; Morley 2011). Although glycogen reserves of cercariae are primarily stored in the tail, a meta-analysis could not find a substantial link between cercarial body and tail size and the survival under different temperatures (Galaktionov and Dobrovolski 2003; Morley 2011). Accordingly, based on our findings and other recent

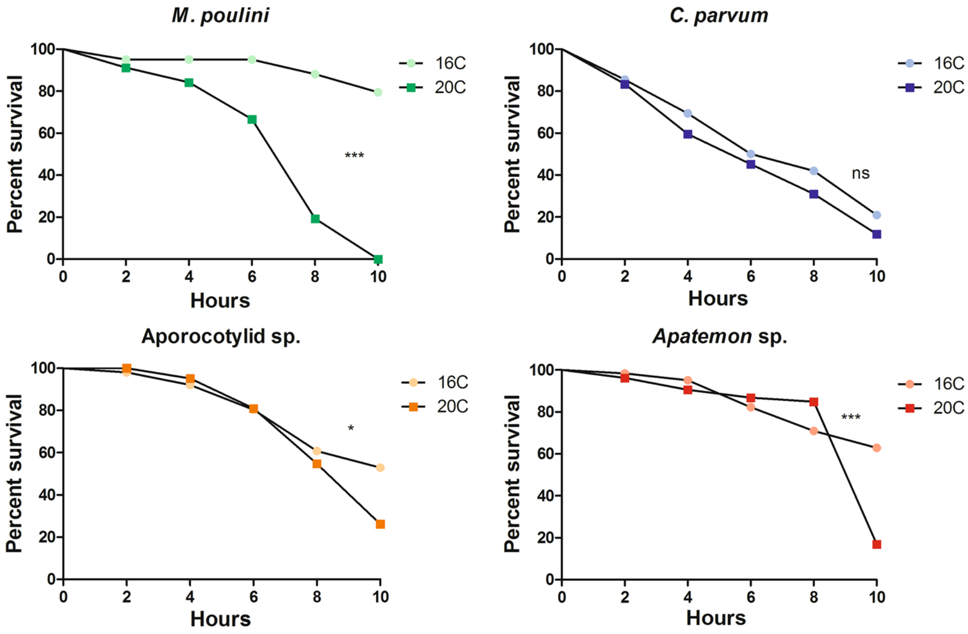

Fig. 4 Survival rates of cercariae 2, 4, 6, 8 and 10 h after emergence from their snail host at 16 °C and 20 °C. Asterisks above plots denote statistically significant differences between the survival curves of temperature treatments (*$P < 0.05$; ***$P < 0.001$; *ns* not significant; Mantel–Cox test). Sample size for each treatment $N \geq 40$

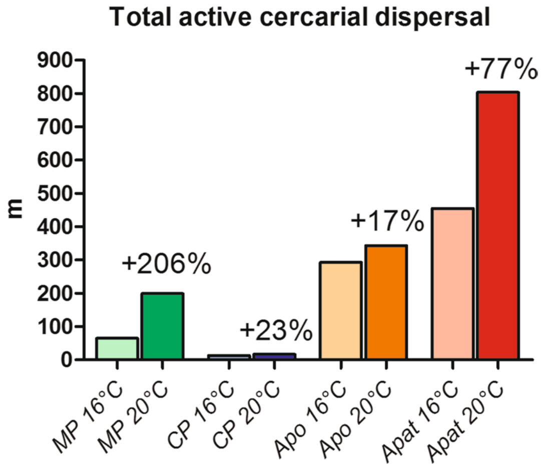

Fig. 5 Total active cercarial dispersal per day to compare the net effects of temperature changes on the dispersal capabilities of trematode cercariae. Each bar represents the sum of the distance travelled by all the cercariae emerged from a single snail over the period of 24 h, accounting for their unequal survival. *MP Maritrema poulini*, *CP Coitocaecum parvum*, *Apo Aporocotylid* sp. I, *Apat Apatemon* sp.

studies on cercarial swimming performance (see Morley 2020), the parasites' target-host identity and the respective host-searching behaviour seem to be an important determinant of their performance under changing temperature conditions.

Overall, we expected a positive net effect on the dispersal capabilities of individual cercariae at higher temperature. Based on the composite index of total active cercarial dispersal, our results support this prediction and show that increases in temperature positively affect the transmission dynamics of all cercariae in our system. The main reason for this pattern is the increased cercarial productivity in all species that offsets the disadvantages of reduced survival time and movement, e.g. in *Apatemon* sp. and *Aporocotylid* sp. I. Accordingly, the species with the greatest increase in cercarial output (*M. poulini*) showed the highest overall benefit under higher temperatures. Altogether, the boost in transmission dynamics varied widely among the different trematode species. However, large percentages of cercariae of *Apatemon* sp. and *M. poulini* were alive after 10 h in the cold treatment survival experiment. It therefore remains to be tested, if the transmission potential of these species could catch up under cold conditions, and if the cercariae remain infective after this period (see Thieltges and Rick 2006).

High variability in transmission dynamics under different temperatures among species, e.g. ranging from slight reductions to 2000-fold increases in cercarial productivity, have previously been reported in various synopses (Poulin 2006; Morley and Lewis 2013; Marcogliese 2016), and from individual studies on marine host–parasite systems (Koprivnikar and Poulin 2009). However, while it is not surprising that different trematode species from various climate zones and habitats, or from different snail hosts show a high interspecific variability, this study for the first time assesses the impact of temperature changes on a diverse parasite community within the same habitat.

Although transmission of all four species tested is expected to increase under warmer conditions, the different species-specific transmission abilities as well as the varying individual patterns of productivity, movement and longevity are likely to impact the composition of the parasite community in this habitat under future climate changes. To interpret these potential changes, we must take the different life cycles and target hosts of the parasites into account. While *C. parvum* and *M. poulini* infect small crustaceans that are abundant and typically occur in high densities in the littoral zones (Fenwick 2001; Friesen et al. 2017), *Apatemon* sp. and *Aporocotylid* sp. I require fishes as second intermediate and definitive hosts, respectively, that are much sparser in the aquatic environment (Selbach and Poulin 2018). In particular, the ability of *M. poulini* to drastically increase cercarial production during warmer temperatures makes this species well adapted to benefit from climate change-related temperature increases. Due to the high density of suitable crustacean hosts that occur in small-scale sympatry with the snail hosts, infections are likely to occur shortly after cercariae emerged from snails. In this case, reduced cercarial survival time is less likely to offset the infection success in their target host. We therefore expect *M. poulini* prevalence and infection intensity in crustacean populations to increase under current global warming trends in the local ecosystems. In marine systems, the closely related trematode *Maritrema novaezealandensis* has been shown to have strong detrimental impacts on coastal ecosystems, leading to reductions in amphipod abundances and species diversity, and to almost complete parasite-induced extinction of amphipod communities under simulated global warming and heat wave scenarios (Mouritsen et al. 2018). This highlights how even single parasite species can have potentially far-reaching impacts and lead to tipping points for ecological communities.

Trematodes occur in aquatic habitats around the world and comprise an estimated 25,000 species with a wide variety of life cycles, host groups and transmission behaviours (Esch et al. 2002; Koehler et al. 2012; Morley 2012). Local trematode diversity in freshwater systems can potentially range up to 40 species (e.g.Faltýnková 2005; Gordy et al. 2016; Schwelm et al. 2018, 2020; Selbach et al. 2020). These diverse trematode communities fulfil important ecosystem functions in their habitats, from contributing to a system's biotic productivity (Kuris et al. 2008) to regulating the interaction and food web structure of free-living organisms (Lafferty et al. 2008; Hatcher et al. 2014), or acting as ecosystem engineers (Thomas et al. 1999). A shift in the composition of local trematode faunas, e.g. when transmission, abundance and prevalence of certain species increase disproportionally under climate change, can impact these crucial parasite-mediated ecosystem functions. Moreover, some trematodes cause important diseases of wildlife or humans, such as schistosomiasis or fascioliasis (Mas-Coma et al. 2009). Due to their capacity to affect the functioning of whole ecological communities and their impact on wildlife and human health, a detailed knowledge of how individual species will react to changing environmental conditions is critical to better understand, predict and mitigate such changes.

Naturally, short-term laboratory experiments only provide a snapshot in time and do not necessarily allow to predict parasite transmission dynamics over longer periods. For example, the brief temperature acclimatization of snails used in cercarial emergence experiments can lead to extreme short-term increases in productivity that typically decrease over time (Mas-Coma et al. 2009; Paull et al. 2015). Moreover, higher temperatures can also lead to increased snail mortality and thereby negate increases in cercarial production over longer periods (Paull and Johnson 2011; Paull et al. 2015). However, even short-lived peaks in cercarial emergence can be sufficient to severely increase the numbers of trematodes that reach the downstream host (Poulin 2006). In particular, since extreme weather events are expected to increase in the future and global climate change will lead to more frequent and more intense heat waves (Meehl and Tebaldi 2004; Coumou and Rahmstorf 2012), the short-term scenarios tested in laboratory settings offer valuable insights into the transmission processes under such erratic temperature changes, especially for organisms in littoral zones that are more susceptible to such variations.

The temperatures used in our experiments do not represent extreme scenarios but fall within the daily ranges of what snails and parasites experience on summer days in the studied coastal lakes that experience regular tidal fluctuations (Hall and Burns 2002; Friesen et al. 2018). However, under extremely high temperatures, beyond the parasites' optimum ranges, a decline in cercarial emergence rates can be expected (Morley and Lewis 2013). Accordingly, the results from one ecosystem are not directly transferable to other host–parasite systems, e.g. in tropical climate zones, where the temperature optima for transmission processes can be highly different (Altizer et al. 2013; Morley and Lewis 2013). However, we show that individual trematode species within the same system react very differently to these changes and there is no reason to assume this would be different for parasite communities in other habitats, where transmission of some species may increase more than others.

In this study, we tested the effects of temperature on the productivity, movement and survival of cercariae as an indicator of the parasites' transmission potential. Yet successful transmission to and infection of the target host consist of a complex series of processes that includes intricate host-recognition and invasion strategies. For example, cercariae show distinctive movement in the vertical water column to maximize host encounters (Haas et al. 2008), and react to specific environmental and host cues, such as local chemical gradients emitted from target hosts (Haas 2003). It remains to be tested how and to what extent the detection of volatile chemical compounds will be affected by varying water temperatures. Given the high diversity of species-specific host recognition strategies (Haas 2003), we expect climate changes to potentially further enhance the differences between trematode species. Beyond the interspecific differences shown in our study, it would be interesting to investigate how mixed-clone infections of the same trematode species co-occurring within a single host individual react to changing environmental conditions (see Lagrue et al. 2007).

Additionally, temperature changes will not only impact transmission stages but will also affect ecological networks, i.e. all parasite stages, hosts and interacting non-host organisms. For example, host abundance, behaviour and mortality, as well as the actual infectivity of the parasites will be impacted under changing climate conditions and thereby influence disease transmission dynamics (Marcogliese 2001; Thieltges and Rick 2006; Mas-Coma et al. 2009; Studer et al. 2010; Paull and Johnson 2011). Therefore, to accurately predict future changes in disease patterns in variable-temperature environments, it will be crucial to consider the thermal responses of both parasites and hosts (Altman et al. 2016), as well as the interactive effects of non-host organisms, such as predators that can interfere with trematode transmission (Goedknegt et al. 2015; Selbach et al. 2019; Vielma et al. 2019; Gopko et al. 2020).

While important human and livestock disease agents, such as *Plasmodium* spp. or *Trypanosoma* spp. understandably receive increased attention with regard to the expected impacts of climate change and global warming (e.g. Franklinos et al. 2019), other parasitic taxa often lack this level of resolution, despite their important roles in ecosystems. However, there is no reason to assume that different species of parasites with different life cycle strategies will react similarly to changing environmental condition, just as one would not expect other related taxa to do so, for example large mammals that share similar habitats (Mitchell et al. 2018). Understanding these species-specific parasite transmission traits therefore remains a fundamental requirement to predict and model future shifts and changes in parasite and disease dynamics in changing environments.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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